The American Midland Naturalist

Published Bi-Monthly by The University of Notre Dame, Notre Dame, Indiana

VOL. 30 NOVEMBER, 1943 NO. 3

William Albert Setchell[1]

Francis Drouet

On April 5th, 1943, William Albert Setchell, professor of botany emeritus in the University of California, died.

He was born at Norwich, Connecticut, on April 15th, 1864. Having shown an early predilection for the study of plants, he took a course in botany while a student in the Norwich Free Academy. He began at this time to collect seriously in the flora of the region and at the age of 19 published privately with George R. Case *A Catalogue of Wild Plants Growing in Norwich and Vicinity* (Norwich, 1883). He also gathered seaweeds on the eastern Connecticut shore and named them according to such manuals as were then available. In 1883 he entered Yale University, where he received much encouragement in botanical pursuits from Professor Daniel Cady Eaton. With free access to Eaton's herbarium and library, he occupied his spare time collecting and determining vascular plants and marine algae. But constantly associating here with W. E. Safford, then a student under Eaton, and with Isaac Holden of Bridgeport, Setchell found his interest and attention directed more and more to the algae. He received his A.B. at Yale in 1887 and entered Harvard University as a Morgan fellow in the fall of that year. He remained there for four years, serving as assistant in biology during the period 1888-91 and receiving the degree of Doctor of Philosophy in 1890. While at Harvard he worked under the stimulating and enthusiastic guidance of William Gilson Farlow, who from all indications considered Setchell his most promising student. Here began the flow of phycological papers that has come almost continuously from his pen for half a century. In addition to taking general courses in botany and zoology, he worked on the morphology and life histories of *Sacchariza dermatodea* (Pyl.) J. Ag. and *Tuomeya fluviatilis* Harv. Part of his time was devoted to work on the smuts, chiefly in the genus Doassansia. He was associated here in collecting and study of the algae with Kingo Miyabe, W. C.

1 Acknowledgment should be made of the sources of information of this account: the biography of Setchell by T. H. Goodspeed in *Essays in Geobotany in Honor of William Albert Setchell* (Univ. Calif. Press, Berkeley. 1936); the many published writings of Setchell, especially his numerous sketches of the lives of American phycologists, most of which are listed in the above work; and my personal correspondence with Setchell.

Sturgis, and others of Farlow's students and with that amazingly professional amateur phycologist, Frank S. Collins of Malden.

From 1891 until 1895 Setchell taught at Yale University. In the summers he instructed in the course in algae at the Marine Biological Laboratory, Woods Hole, the summer retreat of most eastern American students of algae of that day. While at Yale he prepared for publication his classic treatise on the taxonomy and geographic distribution of the Laminariaceae (Trans. Conn. Acad. 9:333-375. 1893), in which he first proposed the ideas of the influence of temperatures of the water upon geographic distribution of species of marine algae that left their impression or were further elaborated in most of his subsequent writings on systematics and distribution. In 1895, Collins, Holden, and Setchell started the publication of bound sets of specimens of North American algae under the title *Phycotheca Boreali-americana*. Although Collins did most of the editorial work on this series, Setchell contributed hundreds of specimens and notes to it during the twenty-three years of its existence.

Setchell was appointed professor of botany in the University of California in 1895 as successor to the late Edward Lee Greene, a position which he retained until his retirement in 1934. During the first year at Berkeley the late Marshall Avery Howe was also on the staff; it was about this time that Howe first evidenced a profound interest in marine algae, and we may presume that this interest was not discouraged by Setchell. At first Setchell's main attention was taken with microscopic algae, in continuation of work started at Yale. His few publications on myxophyceae appearing from 1895 until 1899 are perhaps the most illuminating written on the North American species of this group. This preoccupation with the blue-green algae was later demonstrated in his studies of the vegetation of hot springs (details of which unfortunately were never published) and in general treatments of the algae of the Pacific coast and ocean; it was subsequently transferred to his colleague N. L. Gardner, some of whose major publications were devoted exclusively to the group. That Setchell's sympathy toward work on myxophyceae was still active during the last few years of his life is well shown by his constant and solicitous encouragement of my own work.

Setchell's chief interest soon became the general study of the marine algae of the Pacific coast of North America. In 1897 a correspondence was begun with him by the late Nathaniel Lyon Gardner, who was then teaching school on Whidbey island, Washington, collecting and studying the algae of Puget sound. From 1900 until his death in 1937, Gardner was almost continuously associated with Setchell, first as student, then as collaborator, in the study of the Pacific coast marine flora. In 1899 Setchell collected in Alaska and the Bering sea on the Harriman Alaska expedition; in 1900 he collected in the Hawaiian islands. With Gardner he published a preliminary survey of the algae of northwestern America in Univ. Calif. Publ. Bot. 1:165-418 (1903). In 1903-04 he made a trip around the world, studying in herbaria and collecting marine algae. In 1908 and 1911 other trips were made to European herbaria to study

historic collections. On these visits to Europe he became personally acquainted with many of the phycologists, among others Edouard Bornet and Maurice Gomont, with whom he had long been in correspondence. Until about 1920 he and Gardner were actively engaged in monographic and revisional studies of North American marine algae, all leading to the *opus magnum* entitled "The marine algae of the Pacific coast of North America," three parts of which, treating the blue-green, green, and brown algae, appeared in 1919, 1920, and 1925 respectively in Univ. Calif. Publ. Bot., vol. 8. The remaining part, on the red algae, is still unfinished; but it is hoped that the manuscript can be prepared for publication by Setchell's students and co-workers. In the 1920's Setchell and Gardner also worked on and published floristic papers concerning the marine algae collected during the various expeditions from the California Academy of Science to the west coast of Mexico and the Galapagos islands.

During the years 1920-29 Setchell made a number of trips to the Pacific islands, the Orient, Malaysia, and Australia, collecting extensively and investigating especially the role of marine algae in the formation of various types of coral reefs. This new line of interest was initiated on a visit to the Samoa islands with Mrs. Setchell in 1920 under the auspices of the Carnegie Institution of Washington; a general report of the observations made is to be found in Publ. Carnegie Inst. Wash., vol. 20 (1924). Journeys were undertaken to Tahiti with Mrs. Setchell and Professor H. E. Parks in 1922 and to the Hawaiian islands with Mrs. Setchell in 1924, the object being further studies of reefs. He made a second trip around the world in 1926-27, stopping to collect at Fiji and other Pacific islands, attending the Third Pacific Science Congress at Tokyo, collecting at Hong Kong, visiting Malaysia, Australia, New Zealand, and South Africa. In 1929 he attended the Fourth Pacific Science Congress held in Java and made further collections and studies on the Great Barrier reef of eastern Australia and on Rarotonga. Comprehensive reports were published on the algae of the earlier trips; but unfortunately the only printed documents concerning the collections and observations of the later trips are a number of short and general discussions of the history and classification of reefs, the parts played by the nullipore corallines in the growth of reefs, and problems connected with the origin and spread of insular floras.

The summers of 1931 and 1932 were spent in various parts of Alaska with Mrs. Setchell, attention being given there to the distribution of species of Salix and to general collecting. From that time on Setchell was engaged in working over material collected on earlier trips and especially on the manuscript of part iv. of the "Marine algae of the Pacific coast." After the deaths of Mrs. Setchell and Professor Gardner, he became an invalid himself but continued writing at home and visiting the laboratory as often as he was able. This activity was unabated even during the last year of his life, as his many recent and posthumous publications will attest.

Numerous subjects other than phycology attracted Setchell. His early interest in vascular plants at Norwich and Yale laid the foundation for later

work on marine spermatophytes and for vegetational and distributional studies of terrestrial vascular plants. Following in the footsteps of Farlow, he published on certain of the Uredinales at both Harvard and Yale; at the University of California he encouraged the building up of large mycological collections and made original contributions to the knowledge of certain genera of fungi of California. As director of the botanical garden there, he started the work on hybridization and other studies of tobacco that have been carried on so extensively by his students, Professors R. E. Clausen and T. H. Goodspeed, and by their students. During and after his trips to the south Pacific islands, he became interested in ethnobotany and geobotany and made contributions in these fields. As an administrator and teacher he seems to have been most effective. Botanists and others who knew him at Berkeley and elsewhere and were blessed with his personal regard will acknowledge that with Setchell passed one of their most sympathetic friends.

The monument which, in the estimation of the phycologists of the future, will most honor the name of William Albert Setchell — and along with his, that of his colleague Nathaniel Lyon Gardner — is the magnificent collection of algae accumulated through his efforts or under his direction in the Herbarium of the University of California. But his students and the many others who loved him will perhaps feel that a greater monument stands in their hearts.

FIELD MUSEUM OF NATURAL HISTORY,
CHICAGO, ILL.

A Study, Anatomical and Taxonomic, of the Genera of Rhododendroideae

Herbert F. Copeland

For some years I have been studying the order Bicornes or Ericales, and I have come to entertain the hope of surveying the anatomical characters, and applying them to the classification, throughout the group.

A hint as to this hope was conveyed to my valued correspondent, Dr. W. H. Camp, of the New York Botanical Garden. He responded by placing in my hands his entire collection of preserved material of the group, representing nearly a hundred species, with the explanation that he had found it necessary to suspend his anatomical studies. Part of this material has been used in completing an account of the North American Monotropoideae (18). Because the Rhododendroideae are among the more primitive Bicornes, and are well represented in Dr. Camp's collection and in my own, this group was selected as the next to be studied.

Further material was needed, and I have laid a burden of importunity upon several other correspondents. I am indeed appreciative of the friendliness with which they have endured this and responded to it. I refer to Dr. Wilbur H. Duncan, of the University of Georgia (now in the service of his country); Dr. Noe Higinbotham, of Columbia University; Dr. Donald Wyman, acting for Dr. E. D. Merrill and the Arnold Arboretum; Mrs. Maxcine Williams and Mrs. Lucille Stonehouse, of the Juneau Botanical Club, of Juneau, Alaska; and Mr. P. H. Brydon, of the University of California Botanical Garden.

It is the least of the troubles of these times that I have been unable to draw help from Europe and Asia. Four genera of Rhododendroideae are known to me only by herbarium material, and one by literature only.

For access to herbarium material I am more than ever indebted to the Herbarium of the University of California.

Many botanists (as I) have found the Bicornes subjectively appealing, and the literature of the Rhododendroideae is so extensive that I have made no attempt to compile all references. I hope to have taken account of all that are of cardinal importance. I have refrained from entering citations without personal confirmation, either by myself or by one or another among a number of individuals and institutions which have been generous in giving bibliographic help. These include Dr. E. B. Copeland; the library of the University of California; the California State Library; the Library of Congress; the New York Botanical Garden; the Arnold Arboretum; and the libraries of the United

States Department of Agriculture and the United States Geological Survey. To all these, I offer cordial thanks.

The Rhododendroideae in General

The group here considered was recognized as a taxonomic entity more than a century and a half ago, but its accepted name is only about half a century old:

Subfamily RHODODENDROIDEAE Breitfeld in Engler's Bot. Jahrb. 9:319. 1888; Drude in Engler et Prantl Nat. Pflanzenfam. 4(1):31. 1889.

Ordo *Rhododendra* Jussieu Gen. Pl. 158. 1789.

Ordo *Rhodoraceae* Ventenat Tabl. 2:449. 1799; Klotzsch in Linnaea 24:12. 1851; Eichler Blüthendiagramme 1:342. 1875.

Ordo *Rhododendreae* ("*Ordnung Rhododendreen*") Sprengel Anleit. ed. 2, 2:508. 1818.

Tribus *Rhodoreae* D. Don in Edinburgh New Phil. Jour. 17:152. 1834; G. Don Gen. Syst. 3:842. 1834; Reichenbach Handb. 206. 1837; de Candolle Prodr. 7(2):712. 1839; Gray Man. 267. 1848; Bentham et Hooker Gen. Pl. 2:595. 1876.

Subordo *Rhododendreae* Endlicher Gen. Pl. 758. 1836—1840.

Ordo *Menziesiaceae* Klotzsch in Linnaea 24:11. 1851.

Tribus *Rhododendreae* Maximowicz in Mem. Acad. Sci. St. Pétersbourg sér. 7, vol. 16, no. 9: 2. 1870; Gray Syn. Fl. 2(1):16. 1878.

The accepted name conforms to Engler's practice in the naming of subfamilies; Breitfeld and Drude, who applied it, were among Engler's associates. Breitfeld's publication was inadequate in several respects: it appeared in an essentially anatomical contribution; there is no formal description; and the assignment to a category is indefinite: it is a "Familie, oder, wenn man lieber will Unterfamilie." For such reasons, Dalla Torre and Harms (20) are perhaps justified in citing Drude as formally the author.

The group is defined by corollas deciduous after anthesis, anthers without horns, and septicidally dehiscent capsular fruits. The two former characters may be regarded as negative, and are shared with other Bicornes; the last is the positive common and exclusive mark of the group.

I know of only two previous contributions concerned particularly with this group, being those of Maximowicz (67) and Breitfeld (9). There is, however, much pertinent information in contributions of broader or narrower scope. The last survey of the subfamily as a whole is in Drude's treatment of the entire order, published about fifty years ago. I have used this throughout my work as a guide and point of departure. An important subsequent taxonomic treatment is that of the North American representatives by Small (95). The contributions of Rehder, in Bailey's Cyclopedias (80, 81) amount to additional

monographs. Important contributions to the anatomy include those of Peltrisot (75) and Samuelson (88), on the embryogeny; of Hagerup (39), on chromosome numbers and other matters; of Artopoeus (2) and of Matthews and Knox (63), on the detailed structure of the anthers.

For the sake of reference in the remainder of the general account of the group, it seems necessary at this point to anticipate some of the conclusions of the subsequent special account. Drude recognized seventeen genera, and there has been but one addition on the basis of new material, the *Kalmiopsis* of Rehder. It appears, however, that Bentham and Hooker were correct in reducing *Tripetaleia* to *Elliottia,* and that *Kalmiopsis* is to be reduced to *Rhodothamnus* (**Rhodothamnus Leachianus** (Henderson *sub Rhododendro,* Rehder *sub Kalmiopside*) Copeland f. comb. nov.). On the other hand, the extensive genus *Rhododendron,* as most authorities have understood it, is here divided into five. The outcome is the following list of twenty genera: *Bejaria, Elliottia, Cladothamnus, Rhodothamnus, Dendrium, Diplarche, Kalmia, Phyllodoce, Loiseleuria, Bryanthus, Ledothamnus, Daboecia, Tsusiophyllum, Menziesia, Azalea, Azaleastrum, Therorhodion, Rhododendron, Ledum, Hymenanthes.*

The Rhododendroideae, like most Bicornes, are woody. In stature, they range from small shrubs (arctic, alpine, or epiphytic) to small trees. The leaves are generally alternate, varying to opposite in *Kalmia, Dendrium, Loiseleuria,* and *Daboecia* (figs. 80, 112, 123), whorled in *Ledothamnus.* They are always simple, practically always entire (serrate or obscurely or microscopically so in *Elliottia paniculata, Rhodothamnus Chamaecistus,* and *Diplarche*). In further gross characters they are varied; they may be classified, in a rough way, as follows:

I. Broad, often exceeding 2 cm. in width.
   A. Coriaceous, generally evergreen: *Elliottia racemosa,* many species of *Rhododendron,* most species of *Hymenanthes.*
   B. Herbaceous, generally deciduous: *Elliottia paniculata; Menziesia;* most species of *Azalea,* some of *Azaleastrum.*

II. Narrow, rarely exceeding 1.5 cm. in width.
   A. Herbaceous, deciduous or not long persistent, nearly plane: *Cladothamnus, Therorhodion.*
   B. Coriaceous, evergreen.
      1. Plane or nearly so: *Bejaria, Rhodothamnus,* most species of *Kalmia, Dendrium, Tsusiophyllum, Azalea* subgenus *Tsutsutsi,* most species of *Rhododendron, Ledum.*
      2. Revolute but not ericoid: *Kalmia polifolia, Loiseleuria, Daboecia.*
      3. Ericoid, i.e., small, linear, thick in proportion to the width.
         a. Lamina narrowed, not revolute: *Diplarche;* a few species of *Rhododendron,* e.g., *R. taxifolium.*
         b. Lamina closely revolute: *Phyllodoce, Ledothamnus, Bryanthus.*

Hagerup (39) found that the development of flowers, in most of the Bicornes which he studied, is interrupted by a resting period, which occurs in

most cases during the winter before anthesis. At anthesis, then, the flowers are often associated with leaves of the previous year. Maximowicz (67) has emphasized this character, though noting *Bryanthus, Daboecia,* and *Therorhodion* as exceptions. My preserved and dried material has not enabled me to ascertain the state of affairs in many cases; it appears that in *Cladothamnus, Kalmia polifolia,* and *Phyllodoce,* at least, the flowers are associated with leaves of the same year, and that in the tropical and subtropical representatives, *Bejaria, Elliottia,* and *Ledothamnus,* the flowers may be produced by the same cycle of growth as the leaves below them.

There is variation in the degree to which bud scales are differentiated from foliage. A classification by this character together with the form of the inflorescence is as follows.

I. Winter buds covered by foliage leave or reduced foliage leaves.

1. Unbranched bracted racemes are found in some species of *Bejaria,* in some specimens of *Elliottia,* and in *Bryanthus* and *Daboecia.*

2. Branched flower clusters, i.e., panicles, are found in some specimens of *Bejaria racemosa* and in most specimens of *Elliottia.*

3. Terminal flowers, either solitary or accompanied by others from the axils of the highest leaves, which may be more or less reduced, characterize *Cladothamnus* and *Ledothamnus.*

4. Condensed racemes, i.e., corymbs, occur in most species of *Bejaria,* in *Rhodothamnus Leachianus,* and in several species of *Kalmia;* in the last, they may be axillary as well as terminal. In *Diplarche* the terminal inflorescence is so condensed as to be almost capitate at anthesis, but the rachis elongates and makes it spicate in fruit.

5. Some of the above examples of racemes and corymbs are alternatively interpretable as exemplifying solitary flowers in the axils of reduced foliage leaves. Such is the case of *Rhodothamnus Leachianus.* More definite examples of flowers in the axils of reduced foliage leaves are afforded by *Kalmia ericoides, Dendrium,* and *Leiseleuria.*

6. Flowers in the axils of normal foliage leaves: *Rhodothamnus Chamaecistus, Kalmia polifolia, K. hirsuta, Phyllodoce.*

II. Winter buds clad in specialized cataphylls; inflorescence always essentially corymbose. The following constitute a subordinate natural group recognized by most authorities.

1. The corymb (usually many-flowered; sometimes reduced to from one to three flowers) emerges, unaccompanied by foliage leaves, from a swollen terminal bud whose scales fall promptly; the leafy branches emerge from smaller scaly buds in the axils of the highest leaves of the preceding year: *Menziesia, Ledum, Hymenanthes,* most species of *Azalea* and *Rhododendron.*

2. The corymbs, often greatly reduced, emerge from lateral buds, while the terminal bud produces leaves, in *Azaleastrum* and some species of *Rhododendron.*

3. The leafy shoots spring from the axils, not of the highest foliage leaves, but of the lowest cataphylls, in *Tsusiophyllum* and in *Azalea* subgenus *Tsutsutsi.* Flowers few in the clusters.

4. The inflorescence is said to consist of a terminal flower, usually with one or two more from the axils of the highest foliage leaves of the year, all emerging from a terminal bud whose scales are persistent, in *Therorhodion.* Wilson's (107) criticism of this accepted interpretation is given below in the account of the genus.

In the majority of the genera each pedicel bears, or is embraced at the base by, a pair of bractlets. The bractlets are absent in *Cladothamnus, Bryanthus,* and *Daboecia,* and I have not ascertained their presence in *Ledothamnus.*

The flowers are always hypogynous (in *Bejaria racemosa* the ovary is slightly imbedded; fig. 7); normally pentamerous with two whorls of stamens; either choripetalous or sympetalous, either actinomorphic or zygomorphic.

In the definitely zygomorphic flowers of *Tsusiophyllum* and of *Rhododendron* in the currently accepted broad sense, the median petal is the one on the adaxial side of the flower. This is true also of those species of *Menziesia* whose flowers are pentamerous, and of *Ledum,* whose buds, unlike the open flowers, are recognizably zygomorphic. Eichler (26) noted this as a character of the family Rhodoraceae.

As to the remaining genera, my knowledge of the orientation of the flowers is fragmentary: the flowers are actinomorphic, and I did not see, until I had used up too much of the material, that the point required study. I find the median petal definitely on the abaxial side of the flower of *Bejaria* (figs 3, 6), *Rhodothamnus Leachianus* (figs. 65, 66), and *Dendrium* (fig. 76; this contradicts what Drude has shown, 25, fig. 13). Eichler reports the same condition in *Azalea procumbens* (i. e., *Loiseleuria procumbens*).

Deviations from the prevalent pentamery may be listed as follows:

A. Flowers homomerous.

1. Heptamery characterizes the genus *Bejaria,* though pentamery occurs.

2. Tetramery is often observed in the higher flowers of plants to which pentamery is normal, as *Rhodothamnus Leachianus* and *Dendrium* (fig. 83). In several species of *Menziesia* (fig. 146) and in *Bryanthus* and *Daboecia* (fig. 125) all the flowers are tetramerous. In *Bryanthus,* of which I have seen only scant dried material, I could not determine the orientation of the parts. In *Menziesia* and *Daboecia,* the petals are dorsal, ventral, and lateral, to be represented in floral diagram as occupying the points of an *x.* This is not the orientation of tetramerous flowers of monotropoid plants, nor of *Erica* (Drude, 25, fig. 13): in these, it is the sepals that are placed in a cross and the petals in an *x.*

B. Flowers heteromerous.

1. The floral leaves are increased in number, but not in the same degree in all whorls, so that one may find, for example, seven sepals, seven petals, eighteen stamens and twelve carpels, in some species of *Rhododendron* and many of *Hymenanthes.*

2. The sepals are normally five, while the other parts are decreased in number, in *Elliottia.* In *E. racemosa,* the other parts are normally in fours; this is apparently a phase of the frequent tendency toward tetramery discussed above. In *E. paniculata* the other parts are normally in threes.

3. Stamens are lost from the petalad whorl. In various species of *Ledum* and of *Rhododendron* in the accepted broad sense, one may find some specimens with ten stamens, others with some of the petalad stamens missing, and yet others with only the five sepalad stamens. The petalad whorl is completely lost in *Loiseleuria* and *Tsusiophyllum,* in one species each of *Ledothamnus* and *Menziesia,* in many species of *Azalea,* and in some of *Azaleastrum* and *Rhododendron.*

4. The carpels are reduced to three or two in *Dendrium* and in *Loiseleuria.*

The perianth parts require little discussion. Beyond noting as above the zygomorphy of *Rhododendron*, etc., it is enough to say that the petals are separate in *Bejaria, Elliottia, Cladothamnus, Dendrium, Ledothamnus,* and *Ledum.*

Of the stamens, the petalad whorl is always demonstrably the lower or outer. In *Diplarche,* which differs from all other Rhododendroideae and most other Bicornes in having epipetalous stamens, those of the petalad whorl are inserted at a lower level in the corolla or are quite free of it. Whenever in the group there is a differentiation among the stamens, those of this whorl are the less well developed.

The anthers are of various shapes. Described from gross observation, they are always bilobed, with the connective attached to the filament on the dorsal side, usually near the summit, and opening by long slits or by short slits or circular pores near the summit. The results of anatomical study, set forth below, show that the appearances described are in part deceptive.

The ovary is belted at base by a glabrous nectariferous disk, usually projecting as low lobes between the bases of the filaments. Above the disk, it is lobed, with the lobes (in the normal case of pentamery) opposite the petals. At summit it is impressed, with the style inserted in the impression. To this there are a few exceptions: in *Loiseleuria, Daboecia, Menziesia ciliicalyx* (Drude, 25, fig. 25), *Ledum groenlandicum,* and (if I understand the description) *L. columbianum,* the ovary is attenuate into the style.

Each lobe of the ovary is filled by a locule, and this is largely filled by a massive placenta. Ovules are minute and in most cases very numerous; in *Elliottia, Loiseleuria,* and *Daboecia* they are comparatively few. Near the summit, each placenta is divided into two by a radial cleft.

The style is cylindrical. In *Dendrium,* it ends abruptly in a nearly plane stigmatic surface (fig. 88); in most genera it is expanded at the summit to form a definite collar, most conspicuous in *Cladothamnus* (fig. 60) and in *Elliottia paniculata* (figs. 28, 34). The stigmatic surface exhibit radiating clefts as many as the carpels (figs. 88, 100, 166, 167, 187, 223, 229). In most cases there are prominent lobes between these clefts, but in *Cladothamnus* and *Elliottia paniculata* each cleft is bordered on both sides by ridges, so that there are two ridges between each two clefts. The clefts meet in the middle of the stigmatic surface and lead into an open channel traversing the style. The inner surface of this channel is grooved, the grooves being continuations of the clefts on the stigmatic surface and leading to the clefts of the placentae below. The effect of this structure is that the locules are in communication with the outer air.

It is clear from the structure as described that the carpels are opposite the petals, and that their extremities are marked by the clefts upon the stigmatic surface, not by the lobes.

The fruits vary from subglobular (figs. 23, 51, 74, 90, 118) to elongate (figs. 138, 159, 201, 219). During dehiscence one observes in most examples a fleshy or leathery outer coat which contracts and shatters irregularly, expos-

ing a whorl of chartaceous valves forming the dorsal and lateral walls of the locules. The valves change shape and spread apart so as to expose the numerous fine seeds. In short, the fruit is a septicidal capsule. That of *Ledum* (fig. 201) is peculiar in splitting from below upward. In *Kalmiopsis Leachianus*, each valve is split in two at the summit, seeming to foreshadow the septicidal dehiscence of the Andromedeae.

Microscopic observation has been applied particularly to stems in their first year, leaves, receptacles of flowers, anthers, and ovules and developing seeds; incidentally also to other structures.

Pubescence of the same types is found on stems, leaves, and flower parts (not necessarily on all parts in any one species). The following outline of the types is in general agreement with the accounts of Vesque (105) and Breitfeld (9).

1. Unicellular hairs occur in every species examined (figs. 26, 27, 113, 124, 141, 171, 172, 191, 212, 225). They are thick-walled extensions of epidermal cells, notably frequent upon the bases of filaments, and, in *Menziesia* and *Rhododendron*, as ciliate margins of the cataphylls. I have not seen prickles which are mere outgrowths of the cell wall, as ascribed by Breitfeld to *Kalmia glauca* (i. e., *K. polifolia*, of which I have studied the var. *microphylla*). I suppose that his report was mistaken; that he overlooked, in these prickles, an exceptionally narrow lumen.

2. Uniseriate hairs, branched or unbranched, are exceptional. In this connection, I suspect Breitfeld of two errors. The uniseriate hair, ascribed to the species of *Kalmia* just mentioned, may represent a unicellular hair containing a row of granules of tannin. The much-branched hair, resembling one of *Verbascum*, which he found upon an unidentified species supposedly of *Rhododendron*, resembles nothing which I have seen in this group. Such things, nevertheless, occur:

a. In *Bejaria* there is an obscure appressed pubescence of more or less branched uniseriate hairs, all of the cells being apparently glandular.
b. Multiseriate hairs may break up distally into uniseriate branches.
c. Stalks of glands are not infrequently reduced to single series of cells.

3. Multiseriate hairs are of several types:

a. If they consist of elongate thick-walled cells and are unbranched, they may be called bristles. These occur notably in *Bejaria*, some species of *Kalmia*, *Daboecia*, *Tsusiophyllum*, *Menziesia*, *Azalea* (figs. 161, 162; flattened in subgenus *Tsutsutsi*), and to some extent in *Rhododendron* and *Ledum*.

b. Branched, they occur notably in *Hymenanthes*, and are discussed in connection with that genus.

c. They are elongate, unbranched, and flexible on the lower surfaces of leaves of *Ledum palustre* and *L. groenlandicum* (fig. 204).

4. Glandular hairs, or, one might better say, glandular bristles, are bristles as just described which terminate in capitate glands. The gland consists of several superimposed whorls of tack-shaped cells, in contact with each other at both extremities but (at maturity) separate at the middles. These structures are absent in *Elliottia* and *Cladothamnus,* and I have not seen them in *Rhododendron* proper nor in *Ledum;* otherwise they occur in every genus (figs. 64, 81, 97, 101, 142, 172, 229). In *Hymenanthes,* a single structure may combine the characters of a bristle and a glandular bristle (fig. 208).

5. "Scales" are modifications of glandular bristles, the head broader and flatter, the stalk usually shorter and biseriate. This description applies to structures which characterize, respectively, *Rhodothamnus Leachianus* (figs. 63, 64), *Rhododendron* (figs. 182, 183), and *Ledum* (figs. 189, 190, 191). It is pointed out below that there are essential resemblances between the scales of *Rhododendron* and *Ledum,* while those of *Rhodothamnus Leachianus* are definitely different.

In the typical young stem, cortex and pith usually consist of two kinds of cells intermixed, small tanniniferous ones with thick walls, and larger, thin-walled lighter-staining ones without tannin but often containing crystals (fig. 210); this was pointed out long ago by Vesque (105). The pericycle is a cylinder of thick-walled fibers (figs. 143, 209). The phellogen is the next cell-layer within this; whether it belongs to pericycle or to phloem is not clear. Primary wood is scant. The secondary wood exhibits abundant uniseriate rays; the longitudinal elements are mostly elongate imperforate cells; among these there are comparatively few slender vessels with oblique-scalariform perforations. These characters have duly been set forth by Solereder (97). The nodes are of course unilacunar, that is, each leaf is supplied by a single bundle leaving a single gap in the stele. Each axillary bud, branch, or flower is supplied in quite ordinary fashion by two traces, one from each side of the leaf gap at its base.

Various deviations from the typical structure just described were observed. Reduction of the cylinder of fibers of pericycle to few layers or to one, which may be broken, is an evident evolutionary tendency. It reaches its limit in the complete absence of a differentiated pericycle from stems of *Loiseleuria* and *Daboecia* (it is, however, recognizable in the peduncle of the latter). In *Hymenanthes,* multiseriate vascular rays were observed. Other deviations will be mentioned as the genera are discussed.

There has been, it seems, no comparative study of the wood of mature stems in this group, and I have let the scattered nature of the references to particular examples, and the difficulty of the technique, deter me from undertaking it.

Breitfeld (9) studied the comparative anatomy of the leaves in an extensive range of species. Some of these, and a variety of others, have been available to me. The leaves are always strongly dorsiventral. In many species, the upper epidermis is of larger cells than the lower and appears to be more or less completely divided into two layers by walls in the frontal plane (figs. 25, 37, 63,

82, 124). I understand this to be a false appearance resulting from the accumulation of certain material in the cells. The stomata are always confined to the lower epidermis (the statement of Mansfeld and Sleumer (62), that *Bejaria racemosa* is exceptional in this character, is not substantiated by my material). The stomata generally project slightly beyond the level of the outer surface of the cuticle; as Breitfeld noted, each pair of guard cells is borne on the outturned ends of a cycle of subsidiary cells. The pore is bounded by a prominent ridge at the outer opening: Vesque (105) recorded this character by saying that the stoma has a large antechamber. There is usually no ridge at the inner opening of the pore; to this statement, a number of exceptions are noted under the respective genera. A certain block of genera, *Kalmia* (not all species), *Bryanthus* (i. e., *Phyllodoce*), *Loiseleuria,* and *Daboecia,* have revolute leaves notably pubescent and containing more than one layer of palisade tissue. In features beyond those just mentioned there is much variation. Breitfeld was able to characterize genera and sections, but there are apparently no further characters either of the group as a whole or of subsidiary natural groups of genera. Further description is accordingly placed under the genera respectively, as are some fragmentary notes on cataphylls.

Description of the anatomy of the flowers may begin with an account of the vascular system. I find no previous account of this structure in this group. In familiar fashion, the vascular supply to the flower originates as two bundles from the sides of the bract trace. These unite to form a cylinder which ascends the pedicel and is interrupted, if at all, only by the departure of traces to the bractlets. In the receptacle, the cylinder flares broadly and emits whorls of bundles to sepals, petals, and stamens; above the origin of these bundles there may or may not be gaps. The vascular tissue remaining after the departure of the stamen bundles is the carpel supply; part of it swings outward, to supply the ovary walls; part swings inward to ascend the central column of the ovary and then outward into the placentae.

In *Bejaria racemosa,* there are three separate bundles, with gaps, to each sepal (fig. 8). This is presumably a primitive character. Cursory examination of other supposedly primitive Bicornes has shown the same character in *Chimaphila,* though not in *Clethra* and *Pyrola;* Wilson (106) indicates it in several Dilleniaceae.

I regard as normal the vascular supply to sepals and petals which consists of just one bundle to each. This is more or less well exemplified by *Elliottia* (figs. 29, 40), *Menziesia* (fig. 147), *Rhododendron* (fig. 188), and *Ledum* (figs. 196, 205). The single bundle ordinarily forks promptly into three. Two comparatively complicated states of affairs are more frequent than this:

In *Azalea* (figs. 170, 174), *Azaleastrum* (fig. 180), and *Hymenanthes* (figs. 216, 227) the main bundles which depart from the stele toward the perianth undergo branching, and the branches anastomose, forming loops, from which the bundles actually supplying the sepals and petals run out. This pattern of perianth supply is apparently associated with a receptacle which is laterally extended and not notably impressed at the base.

In the frequent examples of a receptacle strongly impressed at base, the lateral bundles of the sepals tend to originate as branches of the petal bundles. This pattern is exemplified in diagrammatic perfection by *Rhodothamnus Leachianus* (fig. 67), *Dendrium buxifolium* (fig. 78), *Kalmia* (fig. 92), *Phyllodoce* (figs. 103, 106, 110), and *Daboecia* (fig. 126); less regularly by *Cladothamnus* (fig. 57), *Dendrium Lyoni* (fig. 84), and *Loiseleuria* (fig. 114). One may speculate as to whether it is established by a shifting of the origin of the sepal lateral bundles from the sepal bundles to the petal bundles, or, alternatively, by fusion of the petal bundles with sepal bundles which had been free of others, as in *Bejaria*.

The bundles to the petalad stamens (when these are present, as is the more usual case) are always closely associated with the petal bundles, often adnate to them. The bundles to the sepalad stamens emerge at a level almost always perceptibly higher, and are often separated from the sepal bundles by gaps above the latter.

Of the bundles formed by the stele above the departure of the stamen bundles, the carpel dorsals are notably regular in behavior. They ascend the ovary wall in the median planes of the carpels, opposite the petals (except in the exceptional cases when carpels and petals are not equal in number), dip under the groove about the base of the style (except, of course, in the few cases in which the ovary is attenuate into the style) and ascend the latter in those parts of its circumference where it is a thin layer covering the grooves projecting from the style channel. They fade out in the stigma. I have illustrated a considerable part of this course only in *Elliottia racemosa* (fig. 40). Other bundles of the nectary and ovary wall originate in different fashion in different genera, or may be absent.

Of the anatomy as of the gross structure of sepals and petals little discussion is required. They consist, aside from the veins, of parenchyma, which may or may not contain much tannin, and of an epidermis, glabrous or variously pubescent, often with a finely striate cuticle.

Of the filaments, one notes that their development is delayed, elongation taking place only when the flowers are nearly ready to open; and recalls that they are often densely beset with simple hairs.

The anthers of Bicornes have attracted attention at least ever since Linnaeus named the order for a character of the anthers of many examples, though not of any in the present subfamily. Gray's account of *Schweinitzia* (i. e., *Monotropsis;* 33) cites the conflicting opinions of a number of earlier authorities as to the interpretation to be placed upon the position of the anthers of *Pyrola*. The conclusion there reached is that the anthers of this genus develop in an inverted position and right themselves at maturity. Comparatively recently, there have been two studies of the anatomy of anthers throughout the order, those, namely, of Artopoeus (2) and of Matthews and Knox (63). As noted, the junction of filament and anther is usually high on the outer side of the latter. Here a bundle enters the anther. It traverses the anther to the base. The structure described is characteristic of all Bicornes, though there are exceptions.

The only deviation to be noted among the Rhododendroideae is in *Daboecia*. In this genus, the anther is inserted well below the summit, and the main bundle emits from the point where it turns downward a branch which runs some distance toward the summit. It is evident that the mature anther of Bicornes is inverted, either developed in this position, or, as in *Pyrola* and *Arctostaphylos* (Doyel, 24), assuming it during development. The "base" is the distal end; the "summit," where dehiscence takes place, is the proximal end; the surface toward the interior of the flower is dorsal, and the surface turned outward, against the filament, is ventral.

The epidermis of the anther is tanniniferous except in an area extending from the summit of each lobe downward to a varying distance along the line of the septum between the pollen sacs. This area of non-tanniniferous epidermis represents approximately the area of dehiscence. In many Bicornes, some of the epidermal cells, particularly on the dorsal and ventral edges of the lobes, project as papillae; among Rhododendroideae, this is true only in *Daboecia* (figs. 127–133). Internally, the tissues are those usual in anthers, a mass of parenchyma in connective and septa; pollen mother cells; tapetum and wall cells between the latter and the epidermis. An ordinal character is the failure of the hypodermal wall cells to develop the ribs of a typical endothecium. I have not had good views of fully developed tapetum; it appears that the nuclei divide once, and sometimes again, so that the cells come to have two or more nuclei before beginning to collapse.

Since chromosome numbers are usually determined in dividing pollen mother cells, the numbers observed by Hagerup (39) and Sax (89) may be listed here. I regret not having been able to extend the list. These are haploid numbers:

Kalmia latifolia, 12; *K. glauca* (i.e., *K. polifolia*), 24.
Phyllodoce caerulea, 6.
Dendrium and *Loiseleuria*, each 12.
Azalea, generally 13; *A. canadense and A. calendulacea*, each 26.
Rhododendron, Ledum, and *Hymenanthes*, 13 in all examples studied.

As is well know, the pollen grains remain in tetrads. The exine of each individual grain is marked by the halves of three radiating grooves which continue onto its three associates (fig. 228).

It is furthermore well known that there are exceedingly fine non-cellular viscid threads among the ripe pollen tetrads of *Rhododendron*. Matthews and Knox suggest that these may originate from material included in the pollen mother cells but excluded from the pollen grains. I am unable to say anything on this point. Fedtschenko and Basilevskaja (30) noted the presence of these threads also in other genera. The complete list of those in which they have been observed consists of *Bejaria, Elliottia, Cladothamnus, Menziesia, Azalea Azaleastrum, Rhododendron*, and *Hymenanthes*. They are absent from *Rhodothamnus, Dendrium, Kalmia, Phyllodoce, Loiseleuria, Daboecia*, and *Ledum*. According to my understanding of the relationships, I would expect confidently to find them in *Tsusiophyllum* and *Therorhodion*, and not to find them in *Diplarche, Bryanthus*, or *Ledothamnus*.

The wall cells of the anther, or at least the inner wall cells, and the septa, disappear in preparation for dehiscence. Each cell in turn shrinks and becomes dark-staining, collapses against its neighbor, which has already begun to shrink, and becomes indistinguishable. Artopoeus speaks of these cells as undergoing *Schrumpfung;* collectively, they may be designated as collapse tissue. In some of the genera, the collapse tissue extends to and includes the area of dehiscence.

In other genera, an additional tissue is involved in dehiscence. This is recognizable as the anthers approach maturity by densely granular cell contents; later the cells lose their individuality and become converted into an amorphous, apparently fluid mass. Matthews and Knox suggest that the changes described result form an accumulation of oxalic acid. The tissue has been designated resorption tissue. It forms a varying number of layers of cells, in some circumstances including the epidermis and in others underlying it, along the outer edge of each septum where the epidermis is non-tanniniferous. It may form a column extending through the entire height of the anther, or may be confined to the upper part; and in this part it may be broader than a mere column.

A classification of the Rhododendroideae primarily by the presence or absence of resorption tissue, and secondarily by the shape and extent of the area of dehiscence, is as follows:

I. Resorption tissue present.
  A. Resorption tissue including none of the epidermis; the actual dehiscence by a separation of intact epidermal cells; *Bejaria.*
  B. Resorption tissue involving more or less epidermis.
    1. Resorption tissue broadened above and extending as a narrow band to the base of the anther: *Elliottia, Cladothamnus.*
    2. Resorption tissue a narrow column the height of the anther.
      a. Epidermis involved only near the summit, dehiscence by a narrow slit there: *Rhodothamnus, Kalmia, Phyllodoce.*
      b. Epidermis involved throughout the height of the resorption tissue, anther accordingly splitting throughout its height: *Dendrium, Loiseleuria;* presumably also *Diplarche, Bryanthus, Ledothamnus.*
    3. Resorption tissue a moderately broad area near the summit of the anther, attenuate and extending only briefly downward: *Daboecia.*

II. Resorption tissue absent; dehiscence by collapse tissue involving the epidermis.
  A. Collapse tissue involving an area of epidermis which is broad above and extends as a narrow band to the base of the anther. This structure was not observed, but is presumably exemplified by *Tsusiophyllum.*
  B. Collapse tissue involving an area of epidermis which is broad above and extends only briefly down the anther: *Menziesia.*
  C. Collapse tissue involving only a circular area of epidermis near the summit of the anther: *Azalea, Azaleastrum, Therorhodion, Rhododendron, Ledum, Hymenanthes.*

As Artopoeus has noted, whenever the epidermal area of resorption tissue or collapse tissue is broad, its disappearance completes the process of dehiscence, no contraction of the remaining epidermal cells being necessary. When on the other hand the breaking of the epidermis creates a mere cleft, a contraction of the anther walls is necessary in order to cause this to flare and expose

the pollen. In some such cases, those namely of *Bejaria, Rhodothamnus, Kalmia,* and *Phyllodoce,* there is a more or less definite and extensive hypodermal layer of thick-walled cells in the anther, principally on the side toward the connective and away from the cleft, and affording a fixed mechanical support toward which the laterally contracting epidermal cells are drawn. In others, *Dendrium* and *Loiseleuria,* no such layer is present; the flaring of the pore is effected entirely by the lateral contraction of the epidermal cells.

The bicornous species *Hypopitys Monotropa* Crantz (as I think it correct to call it) was one of the first plants to be well understood embryologically. As to other species of the order, Drude examined the seeds of many and used their characters in classification, but his microtechnique was not refined and he exposed himself to certain sarcasm on the part of Peltrisot. Artopoeus appended to his paper on anthers an account of the development of seeds in *Calluna vulgaris* and a few other species, including no Rhododendroideae. Peltrisot (75) made a painstaking study of the embrogeny of all species of the order available to him, and presented figures unmistakably characteristic of them; the whole account is regrettably defaced by a single significant error pointed out by the next author to be mentioned. This is Samuelsson (88), who has left to his successors, myself included, nothing but the filling in of details. I have examined the ovules in all genera represented in my collection of preserved material, seeds in several, intermediate stages in only a few. Those which I have seen represent an essentially uniform process.

The ovules are anatropous with the micropyles above, below, or lateral, at random. In shape they vary from quite elongate, as in *Bejaria,* through every intermediate condition to nearly spherical, as in *Daboecia* (figs. 36, 89, 107, 137, 153, 154, 181, 200. Those of *Elliotia racemosa* are nearly hemispherical with the flat surface adnate to the placenta; fig. 45). When long and numerous, they are inclined toward the base of the flower and imbricate. Each has a single integument, of more than two layers of cells, but not of many, except in *Daboecia.* When the ovule is ready for fertilization, the outer epidermis is differentiated by an accumulation of tannin in the cells, while the inner is in part differentiated as a jacket layer. The micropylar end of the elongate, normally developed and normally constituted embryo sac projects from the jacket layer.

After fertilization, the synergids and antipodal cells quickly become indistinguishable. The endosperm nucleus formed by triple fusion divides promptly and a cell wall forms near the middle of the endosperm cell and at right angles to its long axis; each of the daughter nuclei divides, and two more transverse walls are formed. The significant error in Peltrosot's account of the embryogeny of Bicornes was his failure to observe that the endosperm is cellular from the beginning. Further cell divisions may not conform to a definite schedule. In general, each cell of the four celled endosperm divides lengthwise twice, forming four (figs. 155, 156).The cells at both ends of the endosperm expand at the expense of the internal integumental cells beyond the end of the jacket layer, and form globular masses, respectively the micropylar and chalazal hautoria. The limits of the cells making up these haustoria break down, and their nuclei may fuse and undergo irregular divisions. The middle part of the

endosperm, enclosed in the jacket layer, retains its normal cellular structure. The integumental cells between the jacket layer and the epidermis are crushed sooner than the jacket layer itself: this gives way laterally as the endosperm expands, but remains narrowly constricted at both ends between the haustoria and the cellular part of the endosperm.

The zygote lies within the micropylar haustorium (fig. 156). It gives rise presently to a filamentous suspensor, whose extremity enters the middle part of the endosperm and begins to form the definitive embryo (figs. 22, 157, 217). Those cells of the middle part of the endosperm which are adjacent to the haustoria now begin to break down. This is apparently a result of pressure by their neighbors together with digestion by the haustoria. The disorganization involves the suspensor, which disappears (fig. 218). The disorganized cells became a plug (the *tampon* of Peltrisot) at each end of the endosperm proper, staining in the same fashion as the adjacent haustorium and continuous with it through the constricted end of the jacket layer.

The embryo becomes a globe several cells thick; as this happens, the crushing of the internal integumental cells lateral to the endosperm is carried to completion or nearly so, and the jacket layer, plugs, and haustoria begin to give way. The embryo becomes cylindrical and develops two cotyledons at the chalazal end.

When the seed is ripe, the ellipsoid endosperm is separated from the epidermal layer only by very few thin-walled empty cells, or only by crushed remnants of cells. It encloses a cylindrical dicotyledonous embryo usually less than a millimeter long. The epidermal cells have the inner lateral walls thickened and pitted, while the outer walls remain thin.

The following are the chief variations in, or deviations from, the embryogenic pattern just described:

1. In *Elliottia* (fig. 49) and *Cladothamnus* (fig. 61), there is no definite jacket layer, and no chalazal haustorium has been discovered. The micropylar haustorium is very prominent; at the chalazal end of the endosperm there is an evident degeneration of cells derived, presumably, from the chalazal cell of the four-celled endosperm.

2. In slender seeds derived from slender ovules, internal integumental cells remain unbroken in the ends of the ripe seed as walls surrounding empty spaces. The haustoria, although collapsed, are not longitudinally compressed. These things are true in *Bejaria, Kalmia* (fig. 96), *Menziesia, Ledum* (figs. 202, 203), and *Rhododendron* in the currently accepted broad sense. In the last, the extended ends of the seeds, one or both, may be rendered plumose by the projecting free ends of epidermal cells. On the other hand, in the subglobular seeds of *Loiseleuria* (figs. 121, 122), all internal integumental cells are crushed and the plugs and haustoria are compressed to the shape of double disks like driven rivets. It is evident from Peltrisot's account of seeds of *Phyllodoce* that they show the transition between the two conditions described.

3. In *Azalea japonica* and *A. mollis,* according to Peltrisot, the seeds are

strongly flattened between placenta and pericarp, and the cotyledons, flattened accordingly, are separated by a plane parallel to the surface of the seeds. I have not in other cases discovered a consistent orientation of the plane separating the cotyledons of the cylindrical embryo.

4. The inner and lateral walls of the epidermal cells vary in thickness and in the abundance and proportions of the pits. The walls are especially thick in *Loiseleuria* and *Daboecia,* and the pits are so long and slender as to be canals (figs. 122, 140). The latter genus exhibits additional peculiarities, which are set forth in the special account below.

In the ovary at the time of fertilization, the locules are lined by some two or three layers of elongate dark-staining cells (fig. 152). In the ripe fruit, these have become converted into thick-walled fibers (figs. 53, 158, 207), which constitute the mechanical endocarp of the capsule. In each septum, the fibrous layers of the two adjacent locules are separate (fig. 206), so that they may readily part from one-another as valves. This layer is not usually formed on the adaxial side of the locules, where the placentae enter. In *Elliottia racemosa* the locules expand in a downward direction during the development of the fruit, so that when it is ripe the placentae are inserted near the top. In this species, the fibrous layer extends some distance up the adaxial sides of the locules (fig. 52).

The foregoing survey of the characters of the Rhododendroideae reveals only one common character distinguishing the group from other Bicornes, being the one by which the subfamily is defined, the septicidal dehiscence. Generic peculiarities have been pointed out, with particular frequency in *Elliottia, Cladothamnus,* and *Daboecia* (those of the first two genera are not in most cases shared by the third). It remains true that the group exhibits a pervading uniformity: so far as induction can yield certainty, the group is certainly natural.

Among the characters in which there is variation, those of the anther afford the most satisfactory basis for a division of the subfamily into tribes. The disadvantage that these characters are recognizable only under the microscope is outweighed by the fact that, so far as living and known plants are concerned, they afford sharp limits to natural groups. Having used the work of Drude as a point of departure and object for detailed criticism, I am bound to point out that the resulting system represents a very moderate amendment of his.

Synopsis of the Tribes

I. Anthers dehiscing by means of resorption tissue and containing fine filaments among the pollen tetrads (Tribe *Ledeae* of Drude, excluding the genus *Ledum*).

A. Resorption tissue not involving the epidermis; anthers opening by short slits; endosperm with haustoria at both ends.

1. **Bejarieae,** tribus nova. Rhododendroideae, antheris texto resorbendo per rimas breves dehiscentibus, fila angustissima inter pollen continentibus, albumine haustoria ad utros extremos gerente. Arbores vel frutices Americae Australis partiumque australium Americae Septentrionalis, foliis coriaceis, floribus

paniculatis, racemosis, vel corymbosis, choripetalis, saepius heptameris, seminibus elongatis.

B. Resorption tissue involving the epidermis, in an area broad above and extending as a narrow band to the base of the anther, which opens accordingly by a slit as long as itself; endosperm without chalazal haustotrium.

2. **Cladothamneae,** tribus nova. Rhododendroideae, antheris texto resorbendo per rimas sibi aequilongas, supra latas, dehiscentibus, fila angustissima inter pollen continentibus; albumen sine hautorio chalazale. Arbores vel frutices quatuor Japoniam, Alascam, Carolinam Australem atque Georgiam incolantes, foliis variis, floribus paniculatis, racemosis, vel solitariis, petalis liberis 3-6 recurvis, seminibus variis.

II. Anthers dehiscing by means of resorption tissue through long or short slits and lacking fine filaments among the pollen tetrads.

3. PHYLLODOCEAE Drude. Subtribe (?) *Chamaeledeae* Reichenbach (85, p. 206) in part; Ordo *Menziesiaceae* Klotzsch, excluding *Menziesia* proper; subtribe *Phyllodoceae* Maximowicz.

III. Anthers dehiscing by means of collapse tissue, through long or short slits or circular pores, containing fine filaments among the pollen tetrads except in *Ledum*.

4. RHODOREAE D. Don. Subtribes (?) *Rhododendreae* and *Ledeae* Reichenbach; Subtribe *Eurhododendreae* Maximowicz; Tribes *Rhododendreae* and (as to the type genus) *Ledeae* Drude.

Tribe I. BEJARIEAE

This tribe includes only the following genus, and the tribal characters are included among the generic.

1. BEJARIA Mutis ex L. f.

In the original publication of the order Bicornes, Linnaeus (58) recognized five genera representing the present subfamily Rhododendroideae, being *Kalmia, Ledum, Azalea, Rhodora,* and *Rhododendron.* The younger Linnaeus described the sixth (the fifth in order among those now maintained, *Rhodora* being included in *Azalea*), under the name *Befaria* (60, p. 152), ascribed to Mutis and applied to a plant supposedly from Mexico. The name as published is meaningless. Thirty years later, Zea and Ventenat (cf. Sprague, 99) explained that Mutis had intended to name the genus in honor of his friend Bejar, that the *j* in the name had been mistaken for an *f*, and that the correct spelling is *Bejaria.* This was accepted during most of the nineteenth century. Subsequent authors have been unable to agree; successive treatments have shown a tendency to use the two spellings alternately (cf. Camp, 14, p. 100), and I continue this tradition by disagreeing with Camp. In citing *Bejaria* Mutis ex L. f. we misquote the younger Linnaeus; in citing *Befaria* Mutis ex L. f. we misquote Mutis; and in citing *Bejaria* Mutis ex Zea we misdate the genus. I write *Bejaria* on the assumption that Mutis is entitled to have his spelling respected, and ascribe publication to Linnaeus f. on the basis set forth by Sprague, that the rules warrant correction of an unintentional error.

Anatomical characters are stated in the following description as observed in a specimen of *Bejaria racemosa* collected in Florida by Camp.

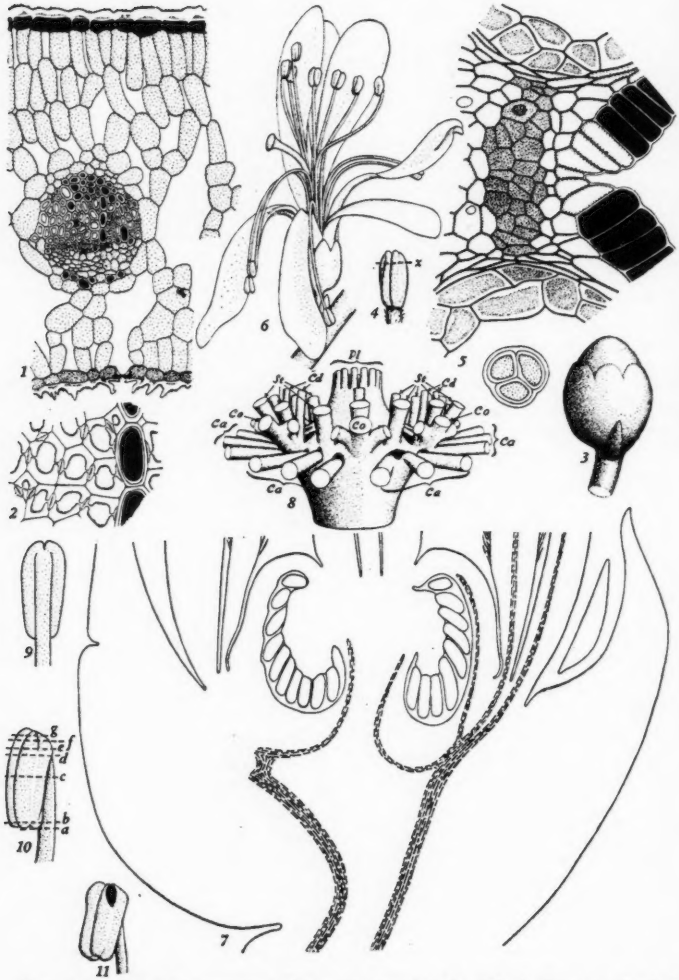
The plants are shrubs or small trees. The pubescence includes elongate simple hairs on the bases of the filaments; and elsewhere (Mansfeld and Sleumer, 62, p. 236) slender crooked filaments of cells, producing a tomentose surface; bristles; and glandular bristles. Mansfeld and Sleumer note that the glands may be deciduous, making it difficult to ascertain their presence in herbarium material. Even in the absence of these, there is often a great deal of resinous exudate on the surface of the plant, apparently from the cells of the tomentum; *B. racemosa* bears the unpoetic common name of "tar flower." In this species, it was seen that the inner epidermis of the calyx is glandular; its secretion is probably not resinous material, but nectar.

In anatomical characters, the stem conforms to the description given in the preceding general section as typical.

The leaf of *B. racemosa* (fig. 1) is about 350 μ thick. On each side is a heavy cuticle thrown into ridges, which are particularly prominent on the lower side. The guard cells are placed at the level of the outer edges of the cells of the lower epidermis, in pits among the ridges of the cuticle. There is no hypodermis: Mansfeld and Sleumer note this character as distinguishing *B. racemosa* from the rest of the genus. There are about three layers of palisade cells. The veins lie imbedded between palisade tissue and spongy tissue; they are bounded above and below by bodies of fibers which are not extended as wings or flanges. Vascular rays are recognizable not only in the midrib but also in smaller veins. The xylem of the veins is of pitted tracheids (fig. 2): this is a surprising and exceptional character.

The flowers are in terminal racemes, or in corymbs which are obviously condensed racemes; comparatively infrequently, secondary racemes at the lower nodes make the inflorescence a panicle. The flower (fig. 6) is choripetalous, essentially hypogynous (the base of the ovary may be slightly imbedded; fig. 7), obscurely zygomorphic, with the odd petal abaxial (figs. 3, 7). Numbers of parts in each whorl may be as few as five or as many as eight; the overwhelming majority of flowers are heptamerous throughout. The calyx is somewhat synsepalous and rather thick and massive. The petals are obovate, oblanceolate, or narrower, white to red. There are two whorls of stamens. The ovary is subglobular, impressed at summit; the style elongate, bent to one side; the stigma capitate or pileoid with a warty surface. The fruit (fig. 23) is a subglobular or pyriform leathery capsule, perhaps 1 cm. in diameter. Many collectors have noted a similarity of flowering plants to *Rhododendron* or *Azalea,* and German authors, to point out a parallel to the *Alpenrose* (*Rhododendron ferrugineum*) have coined for *Bejaria* the common name *Andenrose.*

The vascular system in the floral receptacle is notable for the regular or symmetrical arrangement of bundles all of which are essentially separate (the petalad stamen bundles and carpel dorsals tending to be adnate to the petal bundles; figs. 7, 8), and for the presence of three separate bundles to each sepal.



Figs. 1-11. *Bejaria racemosa*. 1. Cross section of leaf ×160. 2. Portion of vein in fig. 1 ×720. 3. Young bud ×4. 4. Young anther ×8. 5. Portion of cross section of young anther at the level marked *x* in fig. 4, ×320. 6. Flower ×1.6. 7. Longitudinal section of floral receptacle ×20. 8. Vascular system in floral receptacle ×16. *Ca*, sepal bundles; *Co*, petal bundles; *Cd*, carpel dorsals; *St*, stamen bundles; *Pl*, bundles of the central column of the ovary and placentae. 9, 10. Anthers in preservative ×8. 11. Same, dried.

I have illustrated the anther rather extensively (figs. 4, 5, 9–20). The series of diagrams of cross sections shows the hooked vascular bundle and the vertical band of non-tanniniferous epidermis on each lobe. On the young anther, this part of the surface is impressed, shallowly below, as a deep groove above. It is underlain throughout its height by a column of resorption tissue (fig. 5). Traces of this remain as granular matter in the dehiscent anther (shown as stippled areas within the chambers in figs. 14–16). The epidermis does not anywhere undergo collapse or resorption; dehiscence is by the separation of intact epidermal cells along the line of the bottom of the groove on the upper part of each lobe (fig. 19 is from a series in which the next higher section shows a gap between the two cells in the bottom of the groove). Drying the anther causes the cleft to gape widely (fig. 11); a body of thick-walled fiber-like cells on the inside of the lobe on the side away from the cleft (fig. 20) is presumed to have some part in this process. The presence of fine filaments among the pollen tetrads may again be mentioned.

I have not drawn in detail the elongate ovules (fig. 7), their structure being quite normal. Mature seeds have not been seen. It is apparent from young ones showing quite normal stages (figs. 21, 22) that they are elongate, with the ends containing considerable bodies of internal integumental cells.

There have been two recent accounts of the species, Fedtschenko and Basilevskaja (30) recognizing thirty-six, Mansfeld and Sleumer (62) recognizing twenty-five. Camp (14) has reduced one of the latter and added two more.

Bejaria racemosa Ventenat, confined to Florida and Georgia, is the only species occurring in the United States. It is distinguished by the extensive raceme, sometimes compound, of white to pink flowers; by rather small broadly elliptic plane leaves; by lack of glandular hairs; and, anatomically, by the absence of a hypodermis in the leaves. The monographers agree that this species is to be assigned to a distinct section.

Two species are distinguished by elongate leaves with revolute margins, glandular hairs being present: these are *B. cubensis* Griesb., from Cuba, and *B. ledifolia* H. et B., from Colombia and Venezuela.

The remaining great majority of the species are distinguished by characters, extent of inflorescence, color of flowers, pubescence, and size of leaves, which do not in this group afford sharp limits. The great decrease in number of recognized species effected by Mansfeld and Sleumer was accomplished by wholesale reduction to *B. glauca* H. et B., either to varietal status or to complete synonymy. This species and its varieties are abundant at moderate altitudes in the Andes of Colombia, Ecuador, and Peru, and less abundant in Venezuela and Bolivia. The area described is the center of distribution of the genus, inhabited by the majority of the species, and among them by the type species, *B. aestuans* Mutis (all authorities are agreed that the ascription of this species to Mexico was an outright error; it was collected near Bogotá, Colombia). A number of races, treated as of specific rank, are isolated from the main body on Mount Roraima in British Guiana and on Mount Auyan-

Tepui in Venezuela (15). Camp (14) was the first to account for four collections from Central America: he makes two of these a new species, *B. guatemalensis*, and treats the others as atypical representatives of the Mexican species. In Mexico, he recognizes two well-marked species, *B. mexicana* Bentham, glandular, with white flowers, and *B. glauca* (*B. levis* Bentham), non-glandular, with pink to red flowers. *B. Hintonii* is described as probably a stabilized hybrid of these; there is much other hybrid material, all of which may be called *B. discolor* Bentham.

It may be repeated in summary that *Bejaria* shares with *Elliottia* and *Cladothamnus* resorption tissue in the anthers and filaments among the pollen tetrads,

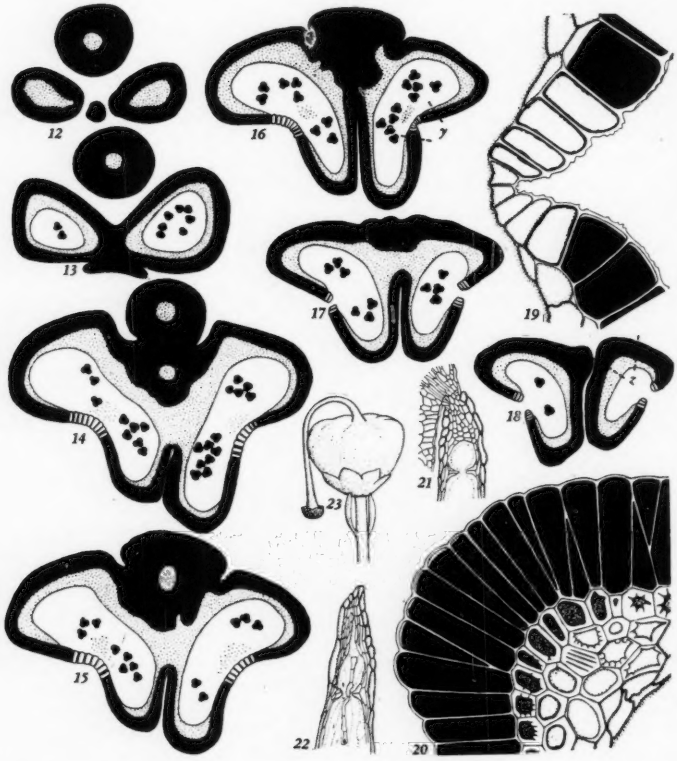


Fig. 12-23. *Bejaria racemosa*. 12-18. Cross sections of anthers at the levels marked a-g in fig. 10, ×40. 19. Area marked *y* in fig. 16, ×320. 20. Area marked *z* in fig. 18, ×320. 21, 22. Micropylar ends of sections of developing seeds ×40. 23. Fruit ×1.6.

a combination of characters found nowhere else; that it differs from *Elliottia* and *Cladothamnus* in having anthers opening by a brief slit and haustoria at both ends of the endosperm; and that it differs from all other Rhododendroideae in anthers which are breached neither by collapse nor by resorption of cells, but by the formation of a cleft between intact cells, and also in the trilacunar vascular supply to the sepals. The genus has generally been regarded as primitive among the Rhododendroideae, and I construe as primitive its characters as just listed. Discussion of its relationships with other supposedly primitive Bicornes is now in order, *Clethra* in particular being brought into comparison. The inflorescence of *Clethra* and its embryogeny (cf. Peltrisot) are much as in *Bejaria*. The wood also is similar, but the young stems show a definite endodermis and have a pericycle which is parenchymatous, not fibrous. Quite speculatively, I would suppose that *Clethra* has lost the fibrous pericycle, and *Bejaria* the differentiated endodermis, of a common ancestor. The position of the anthers of *Clethra* is as in most Bicornes; a prominent endothecium of peculiar structure is present; there are no fibers among the pollen grains, and there is no resorption tissue. I suppose the fibers and resorption tissue to have appeared during the evolution of *Bejaria;* and if the presence of resorption tissue represents a comparative advance, its failure to involve the epidermis is primitive. Similarly, the reduction of the endothecium to a few fibrous cells in the upper part of the anther may be recognized as an advance which has not reached its limit. The pistil of *Clethra* is tricarpellate; it may be that it is derived, not from a pentacarpellate pistil, but from a more primitive gynoecium of separate carpels indefinite in number. It is primitive in that each carpel is represented by a separate stigma (Hunt, 50). The loculicidal dehiscence of the fruit is presumably a derived character. The effect of this comparison is to show that while *Clethra* and the Rhododendroideae are descended from a common ancestor, this ancestor and all transitions between it and the groups named have disappeared, leaving the survivors quite isolated.

Tribe II. CLADOTHAMNEAE

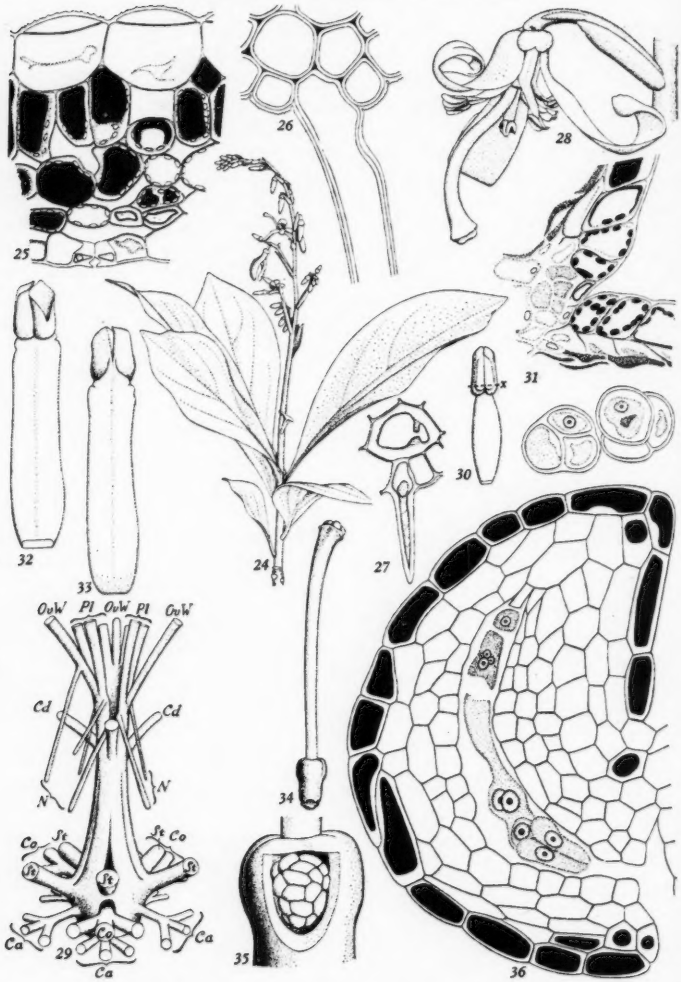
The Cladothamneae are distinguished by anthers opening throughout their length by resorption tissue; by filaments among the pollen tetrads; by peculiarities in the embryogeny; and by flowers with separate petals. They exhibit furthermore a characteristic manner, described below, of discharging the pollen. The four species, of three widely separate areas, form two genera distinguished as follows:

1. Leaves petioled, attenuate at both ends; inflorescence paniculate, flowers usually with four or three petals ..... 2. *Elliottia*

1. Leaves sessile, obtuse; flowers terminal or in the axils of the highest leaves, with five (rarely six) petals ..... 3. *Cladothamnus*

2. ELLIOTTIA Muhlenberg ex Elliott

Publication of the genus which Muhlenberg named for the eminent southern botanist Elliott has been ascribed (20) to Nuttall (70); actually it was by Elliott himself. Only the type species was known to these American authors.



Figs. 24-36. *Elliottia paniculata*. 24. Flowering shoot ×0.8. 25. Cross section of leaf ×320. 26. Simple hair from lower surface of leaf ×320. 27. Simple hair from pedicel ×320. 28. Flower ×4. 29. Vascular system in floral receptacle ×40. *Ca*, sepal bundles; *Co*, petal bundles; *St*, stamen bundles; *Cd*, carpel dorsals; *N*, nectary bundles; *OvW*, Ovary wall bundles; *Pl*, bundles of the central column of the ovary and placentae. 30. Young stamen ×8. 31. Portion of cross section of anther, at the level marked *x* in fig. 30, ×320. 32, 33. Dehisced stamens ×8. 34. Pistil ×4. 35. Upper part of ovary, dissected, ×16. 36. Ovule ×320.

A few years later, Siebold and Zuccarini described *Tripetaleia* as a remarkable novelty from Japan, doubtfully assigned to Olacaceae. An additional species of this genus was described by Maximowicz. Bentham and Hooker reduced *Tripetaleia* to *Elliottia,* and Gray (37) was able to list this among the genera having a discontinuous distribution in eastern Asia and eastern North America. Drude restored *Tripetaleia,* but this was done on the basis of inaccurate information as to the structure of the fruit of the type species of *Elliottia.* The three species are, indeed, different enough so that Bentham and Hooker assigned each of them to a separate section. They are distinguished as follows:

I. Seeds falling from the placentae; petals normally three.
A. Capsule raised above the calyx upon a column shorter than itself.

1. ELLIOTTIA BRACTEATA Bentham and Hooker Gen. Pl. 2:598. 1876. *Tripetaleia bracteata* Maximowicz in Bull. Acad. Sci. St. Pétersbourg 11:433. 1867. Japan.

B. Capsule raised above the calyx upon a column longer than itself.

2. ELLIOTTIA PANICULATA Bentham and Hooker l. c. *Tripetaleia paniculata* S. et Z. in Abh. kgl. bayerischen Akad., math.-phys. Kl., 3:732. 1840. Japan.

II. Seeds adnate to the placentae, petals usuually four.

3. ELLIOTTIA RACEMOSA Muhlenberg ex Elliott Bot. South Carolina and Georgia 1:448. 1817. Lowlands of Georgia and adjacent South Carolina.

For anatomical study, I have had an abundant collection of *E. racemosa* obtained by Dr. Wilbur H. Duncan in Georgia; and a good collection of *E. paniculata* furnished by the Arnold Arboretum. Of *E. bracteata* I have seen nothing.

The plants are shrubs or small trees. Pubescence is exclusively of simple hairs. These produce a hirsute lower surface, on leaves and on the distal ends of petals, of *Elliottia racemosa:* for the rest, this species is glabrous. *E. paniculata* bears fewer such hairs on the leaves (fig. 26) and an abundance of smaller ones (fig. 27) on pedicels, and calyces. The filaments are glabrous in both species.

In the stems there is a very thin cylinder, an incomplete single layer, of fibers of pericycle. *E. racemosa* exhibits a moderately thick layer of primary xylem, consisting of rows of vessels imbedded in thin-walled parenchyma. In the pith of both species, small thick-walled tanniniferous cells tend to predominate, forming a continuous belt within the primary wood of *E. racemosa* and making up almost all of the pith of *E. paniculata.*

The leaves are variable in size and shape. The prevalent shape is elliptic, with attenuate extremities. Sizes tend to be large, five to ten centimeters or more long. Notable anatomical features of the leaves are these: That of *E. paniculata* (fig. 25) is about 125 μ thick, and has a single layer of palisade cells; that of *E. racemosa* (fig. 37) is about twice as thick, and has in most parts

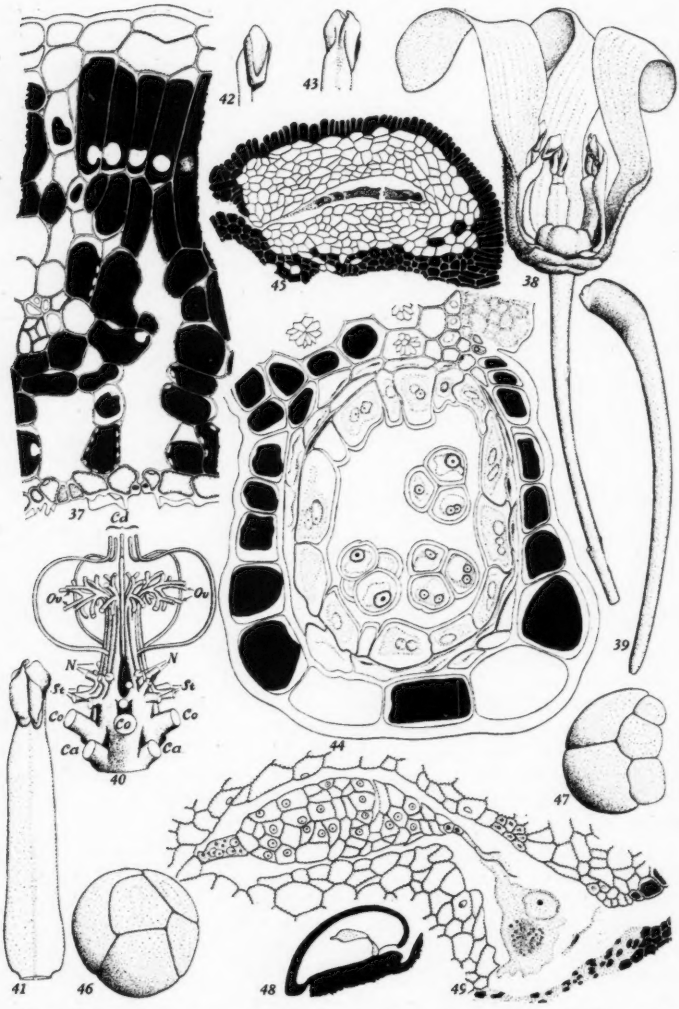


Fig. 37-49. *Elliottia racemosa*. 37. Cross section of leaf ×320. 38. Flower (one petal, three stamens, and the style fallen) ×4. 39. Style and stigma ×4. 40. Vascular system in floral receptacle ×20; labels as in fig. 29. 41-43. Stamen and dehisced anthers ×8. 44. Portion of cross section of young anther ×320. 45. Ovule ×160. 46, 47. Clusters of ovules soon after fertilization ×16. 48. Section of developing seed ×20. 49. Portion of same ×320.

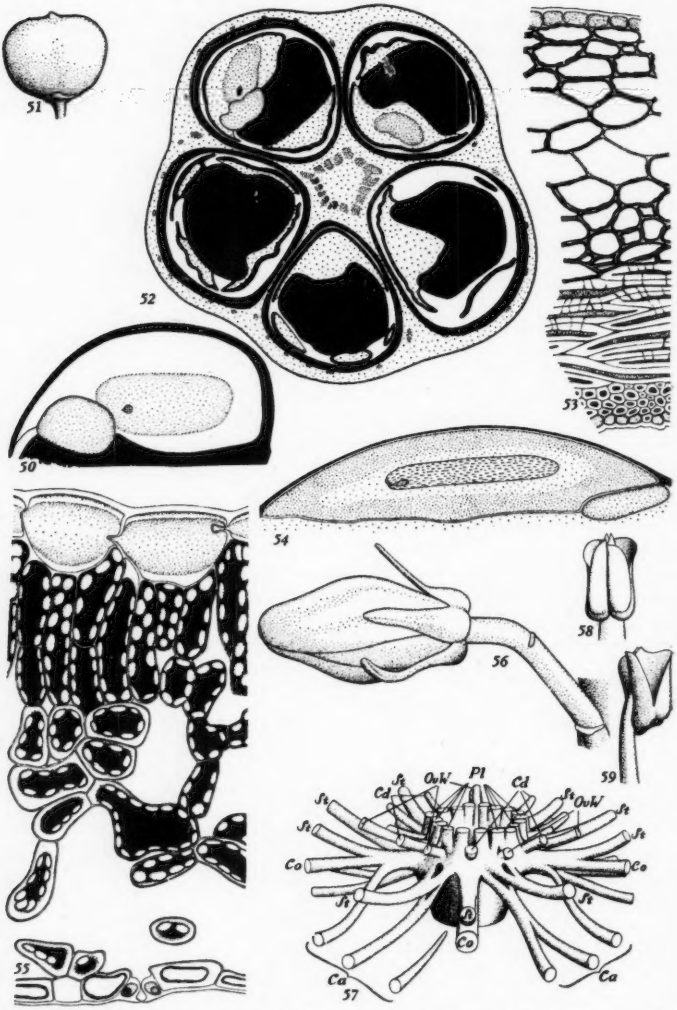
two layers of palisade cells. The cells of the upper epidermis are large. The stomata are placed at the level of the outer edges of the cells of the lower epidermis; in *E. racemosa* a heavy cuticle forms pits about them. In *E. paniculata,* the pore is bounded by an outer ridge and there is no inner ridge; in *E. racemosa,* neither ridge is evident.

The terminal inflorescence (fig. 24) is fundamentally racemose, often becoming paniculate by branching in the lower part. The abundant flowers (figs. 28, 38) are rather small and apparently quite handsome. Of small, somewhat united sepals, most flowers have five. The number of petals in flowers of *E. racemosa* is sometimes five, usually four; in those of *E. paniculata* it is normally three. In the open flowers of both species they are strongly recurved and have spoon-like ends. Of stamens there are twice as many as the petals; the filaments are flattened, in *E. paniculata* at anthesis bent outward. The pistil (figs. 34, 35, 39) is of as many carpels as there are petals. The lower part of the ovary is narrowed and sterile: this part is very brief in *E. racemosa,* longer than the fertile part in *E. paniculata.* The style is stout, bent to one side, longer than the petals. The collar and the ridges bounding the grooves on the stigmatic surface are prominent in *E. paniculata,* obscure in *E. racemosa.*

In the floral receptacle each sepal and petal is supplied by a single bundle which forks promptly into three (figs. 29, 40). The stamen bundles are free of the perianth bundles. Above their departure, the vascular cylinder, as it enters the sterile part of the ovary, contracts into a column, short in *E. racemosa,* long in *E. paniculata.* In the former, the nectary is supplied by brief bundles from the sides of the column; in the latter, the nectary bundles descend from above, from the bases of the carpel dorsals and placental bundles. The carpel dorsals emerge at the base of the fertile part of the ovary.

Along the length of each lobe of the young anther (fig. 30) there is an opaque white band which is narrow below and broadened above to cover almost the whole width of the inner surface of the lobe. This band consists of resorption tissue (fig. 44), involving the epidermis except at the extreme lower end, where it is hypodermal (fig. 31). Dehiscence is accomplished essentially by the disappearance of the resorption tissue, which lays the pollen sacs wide open and allows the pollen to fall out.

In both species, preserved material gave evidence of a certain behavior which is presumed to be an adaptation for pollination.. The flower buds are pandant. When they are nearly ready to open, the pollen falls from each anther as four cylindrical masses, each consisting of pollen tetrads entangled among fine threads. The pollen lodges in the conical apex of the closed corolla, beyond the stigma. The style then elongates and the stigma presses the pollen against the inner surfaces of the petals. At this time the clefts in the stigmatic surface are not open, the ridges bordering each cleft being in contact; the stigma is presumably not receptive; it is supposed that the effect of the behavior described is to fasten the pollen into the spoon-like ends of the petals. It will take study of living plants to make certain of this, and to reveal its significance in the process of pollination.



Figs. 50-54. *Elliottia racemosa*. 50. Section of developing seed × 20. 51. Fruit ×1.6. 52. Cross section of fruit ×8. 53. Cross section of outer wall of fruit ×160. 54. Longitudinal section of seed ×20.

Figs. 55-59. *Cladothamnus pyrolaeflorus*. 55. Cross section of leaf ×320. 56. Bud ×4. 57. Vascular system in floral receptacle ×28; labels as in fig. 29. 58, 59. Dehisced anthers ×8.

In each locule, ovules are rather few: figure 35 shows about fifteen in *E. paniculata;* figure 40 would indicate about eight in *E. racemosa,* but the actual number is usually smaller. The ovule of *E. paniculata* (fig. 36) is elongate, attached to the placenta near the middle of one side; that of *E. racemosa* (fig. 45) is dome-shaped, grown fast to the placenta throughout one surface.

I have several stages in the development of seeds of *E. racemosa,* though not a complete series. Soon after anthesis, one finds that only one or two ovules on each placenta are developing (figs. 46, 47). Presumably, within the developing ovule, the primary endosperm cell divides to form a row of four, and presumably it is the micropylar cell of this row which develops into a large globular haustorium penetrating the placenta (fig. 49). The chalazal haustorium, if any, is abortive; a small body of moribund cells, found at the chalazal end of the endosperm in early stages, may represent the antipodal cells rather than the chalazal cell of the four-celled endosperm. It persists only briefly. The endosperm absorbs all of the integument except the epidermis. This is folded into a narrow wing, two cells thick, at the margin of contact between endosperm and placenta. The embryo develops at the end of a suspensor and becomes linear and dicotyledonous (fig. 54). Meanwhile, the placenta, which is in flower rather inconspicuous, grows considerably, pushing from above downward and in all directions against the lining of the locule, crushing the abortive seeds flat, and forming on the fertile seeds a smooth surface continuous with its own. The fibrous layer lining the locule (fig. 53) develops not only on the abaxial and lateral sides, but also on the adaxial side (fig. 52) except near the summit, where the placenta is attached. The structure described arouses curiosity as to dehiscence and dissemination. I suppose that the capsule valves fall from the placentae like cups, and that the placentae are objects disseminated. The statement that *Elliottia* has only one ovule per locule, on the basis of which Drude maintained *Tripetaleia* as a distinct genus, is ascribed to Planchon. Apparently he mistook for a single seed the placenta with its one adherent fertile seed and several crushed abortive ones.

Siebold and Zuccarini present a figure of a dehiscent fruit of *E. paniculata* in which each locule contains about eight seeds: this suggests that in this species also there is much abortion. The seeds are ellipsoid, without appendages except for a narrowing at the point of attachment. These authors' figure of a section of a seed, showing the radicle pointing away from the point of attachment, is manifestly erroneous.

3. CLADOTHAMNUS Bongard

The genus *Cladothamnus* includes a single species whose nomenclatorial history is complicated only by a single synonym, published a year later than the valid name and promptly withdrawn:

CLADOTHAMNUS PYROLAEFLORUS Bongard in Mem. Acad. Sci. St. Pétersbourg sér. 6, math.-phys., 2:155. 1833. *Tolmiaea occidentalis* Hooker Fl. Bor. Am. 2:44. 1834. Type collected by Mertens near New Archangel (now Sitka). Alaska near the coast and south as far as Oregon, there rare near timberline.

For anatomical study I have a good collection, in flower and somewhat past, made near Juneau by the Juneau Botanical Club.

The plant is a shrub to 2 m. tall. It is almost completely glabrous: there are a few short stiff simple hairs on the stem and as a ciliate margin to the sepals. The stem exhibits no anatomical peculiarities; the cylinder of fibers of pericycle is well developed.

The leaves are deciduous, to 5 cm. long, essentially sessile, narrowly elliptic, cuneate at base, obtuse, often with an apiculation at apex. They are about 250 μ thick (fig. 55). The upper epidermis is of notably large cells, the lower of small ones. The cuticle is thin. Internally there are one or two layers of elongate palisade cells.

Main stems terminate, usually, in an inconspicuous terminal bud. Lateral branchlets, after producing a few leaves, often bear a terminal flower; their highest leaves are then reduced and accountable as bracts, and two or three of these may subtend lateral flowers. There are no branchlets.

The flowers are ordinarily pentamerous, occasionally hexamerous. The receptacle is somewhat impressed at base. The sepals are united at base, attenuate above. The oblong, obtuse, recurved petals are yellowish-red to red. Stamens are twice as many as the petals; the filaments are flattened. It has been noted that the anthers were not accurately described by Bongard: they are attached to the filaments at the middle of the outer side and open by slits which are broad above and extend nearly to the base (figs. 58, 59). The pistil (fig. 60) is of carpels as many as the petals, the ovary depressed-globose, the style long, stout, bent to one side, the collar and the ridges bounding the grooves on the stigmatic surface exceptionally prominent. The flower is indeed very much of the appearance of that of *Pyrola rotundifolia,* though decidedly larger.

In correlation with the impressed base of the receptacle, the main sepal bundles arise almost at the level of the petal bundles and commence their courses in a recurved direction (fig. 57). To each sepal there are also two lateral bundles: these arise very variously: they may spring either from the main sepal bundles, or from the petal bundles, or may originate unattached in the tissue of the receptacle. The petal bundles are recurved at base, though less strongly so than the sepal bundles. The petalad stamen bundles are adnate through some distance to the petal bundles and the sepalad stamen bundles show a tendency to become attached to the main sepal bundles. Above the departure of the sepal bundles, the vascular cylinder contracts to some extent. The carpel dorsals depart at this level; and alternating with them, there departs a whorl of ovary wall or carpel lateral bundles. The remaining vascular tissue supplies the placentae.

The anatomy of the anther is altogether as in *Elliottia,* and I have not illustrated it. Dehiscence and the time and manner of discharge of pollen are likewise the same: the buds are pendant (fig. 56); the pollen is shed before anthesis, from each anther in four masses bound together by fine threads, and

lodges in the end of the corolla. The style then elongates and the stigma, presumably not yet receptive, presses the pollen against the inner surfaces of the apices of the petals. After this, still before anthesis, the growth of the style throws it into the curve which is later so prominent.

Ovules are fairly numerous on each placenta. One finds in developing fruits that the majority of the ovules are not developing. The comparatively few which are functional (fig. 61) show an endosperm with a large micropylar haustorium; this has eaten away enough tissue so that it is in contact with the placenta. There are a few moribund cells at the chalazal end of the endosperm, but there is no evidence of the formation of a chalazal haustorium. The embryo develops at the end of a suspensor in the central, cellular portion of the endosperm.

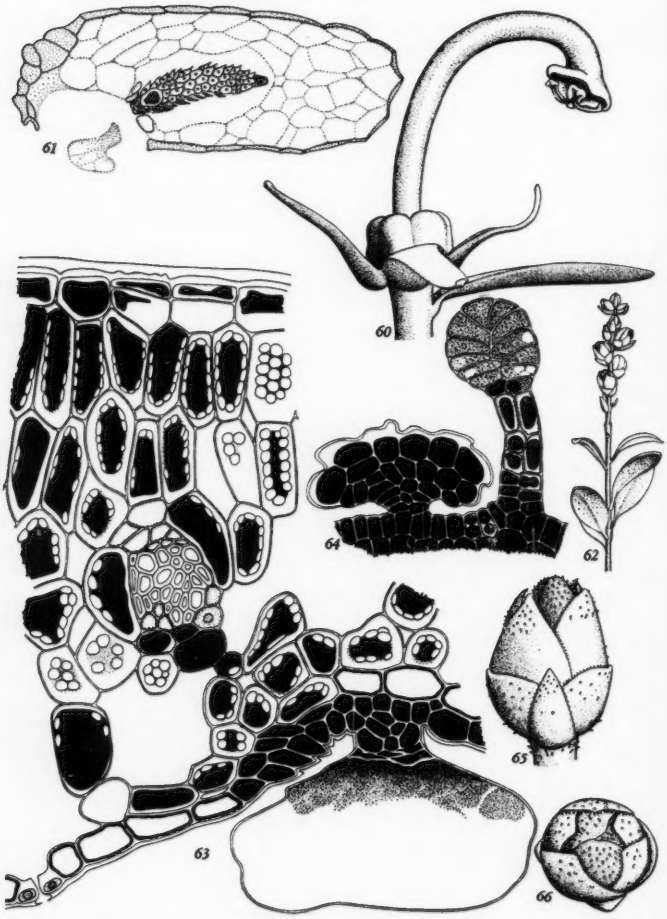
The naturalness of the tribe Cladothamneae as here set up is indicated by the whole range of the characters of each of the three species studied, and their uniformity in structure of anthers and manner of discharging of pollen seems conclusive. Maximowicz had already implied it, in a negative way, by excluding *Cladothamnus* and *Tripetaleia* from his account of the Rhododendreae of eastern Asia.

The group is placed after *Bejaria* on the assumption that the extensive area of resorption tissue, associated, as it is, with an absence of mechanical tissue within the anther, is a derived character. If it may also be assumed that the absence of a chalazal haustorium in the developing seeds is derived, not primitive, one may hold that *Bejaria* represents approximately the ancestry of the group. The one discrepancy is the more perfect union of the extremities of the carpels in *Bejaria,* as if this genus had diverged in this one point from an ancestor shared with the Cladothamneae, while the latter had diverged in several. Such seems to be the conception of the relationships of these groups which best conforms to present knowledge.

Tribe III. PHYLLODOCEAE (Maximowicz) Drude

The tribe Phyllodoceae is definable by a combination of two microscopic characters of the anthers, the presence of resorption tissue involving the epidermis and the absence of filaments among the pollen tetrads. The list of genera as fixed by these characters is precisely the list given by Drude. There are other prevalent characters marking the group as natural, though none of these is quite coextensive with it. The leaves, except in some species of *Kalmia,* are small, buxoid or ericoid. The flowers are regular, and in pentamerous ones, so far as the point has been studied, the median petal is always on the abaxial side. The character of the seeds as given by Drude, that they lack wings or appendages, applies generally, but not to *Kalmia,* and occurs outside this group in *Elliottia paniculata.* Chromosome numbers, so far as they are known, are six, twelve, or twenty-four.

There are nine genera, all small and definitely distinct. They are widely scattered. Thus the tribe exhibits, in moderate degree, the features of a relic group. As in all such groups, one lacks the evidence upon which very definite



Figs. 60, 61. *Cladothamnus pyrolaeflorus*. 60. Flower with petals and stamens fallen ×4. 61. Longitudinal section of developing seed ×80.

Figs. 62-66. *Rhodothamnus Leachianus*. 62. Twig with buds ×0.8. 63. Cross section of leaf ×320. 64. Gland and scale of ovary ×320. 65, 66. Buds ×4.

opinions as to ancestry and mutual relationship might be based. The speculations upon these matters, in accord with which the genera are placed in sequence, will be stated presently. First, in the following artificial key, the list of genera and the outward characters by which they are recognized are given:

1. Petals united.
  2. Anthers opening by brief slits at the summit.
    3. Flowers normally pentamerous, bractlets present.
      4. Anthers not held in outpocketings of the corolla.
        5. Leaves elliptic, the margins not strongly revolute ..... 4. *Rhodothamnus*
        5. Leaves linear, the margins strongly revolute ..... 8. *Phyllodoce*
      4. Anthers, in bud and until soon after anthesis, held in outpocketings of the corolla ..... 7. *Kalmia*
    3. Flowers tetramerous, bractlets absent ..... 12. *Daboecia*
  2. Anthers opening by slits as long as themselves.
    3. Stamens not epipetalous.
      4. Flowers pentamerous, stamens five, leaves obovate, moderately revolute. ..... 9. *Loiseleuria*
      4. Flowers tetramerous, stamens eight, leaves linear, strongly revolute. ..... 10. *Bryanthus*
    3. Stamens, at least those of the sepalad whorl, epipetalous ..... 6. *Diplarche*
1. Petals free, anthers opening by slits as long as themselves.
  2. Leaves elliptic, not revolute ..... 5. *Dendrium*
  2. Leaves linear, strongly revolute ..... 11. *Ledothamnus*

Drude and Small, in accord with phylogenetic ideas which are valid in other groups, have listed first among the genera of this tribe those with choripetalous flowers and anthers opening by long slits. As to the latter character, Samuelsson (88) has pointed out that it is in this group always associated with the complete absence of a mechanical endothecium. Noting further that it is associated with the presence of resorption tissue; and that resorption tissue is presumed to be present in primitive form in *Bejaria*, whose anthers open by brief slits; one concludes that in this group anthers opening by long slits are a derived character. Since choripetaly is found here only in association with anthers opening by long slits, one concludes that this character also is derived. It appears that among the Phyllodoceae sympetaly and anthers opening by short slits are primitive; that the group is derived from something like *Bejaria*, the chief modifications being sympetaly, the involvement of a band of epidermis in the resorption tissue, and the loss of filaments among the pollen tetrads. The relatively primitive genera are *Rhodothamnus*, *Kalmia*, and *Phyllodoce*. None of the three represents a form ancestral to the others. *Kalmia*, with primitive seeds and including several species with fairly large leaves and cormybose inflorescences, is distinguished by a specialized corolla. In *Rhodothamnus*, the small thick leaves seem a derived character. As to *Phyllodoce*, there is no doubt that the linear, strongly revolute leaves are specialized. Meanwhile, the classification of the remaining genera by corolla and anthers seems to yield artificial groups, as if choripetaly and long slits had appeared repeatedly. Not with perfect satisfaction, even perhaps arbitrarily, the genera are here arranged by the nature of the leaves, as suggested by Breitfeld. The result, in outline, is as follows:

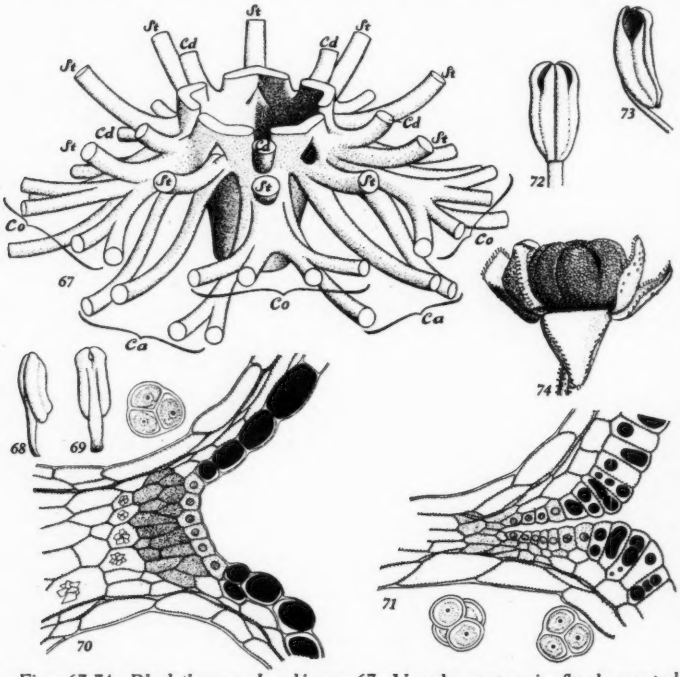
Leaves small and thick, not revolute or scarcely so: *Rhodothamnus, Dendrium, Diplarche.*

Leaves various; corolla with outpocketings in which the anthers are held until some time after the flowers open: *Kalmia.*

Leaves from moderately to very strongly revolute: *Phyllodoce, Loiseleuria, Bryanthus, Ledothamnus, Daboecia.*

4. RHODOTHAMNUS Reichenbach

Among the original species of *Rhododendron* published by Linnaeus, one, a native of the Alps, is decidedly different from the rest; Reichenbach set it apart as constituting the genus *Rhodothamnus*. A hundred years later, Henderson described a similarly divergent *Rhododendron* as occurring on a few peaks in southwestern Oregon. Rehder, after due study, assigned this to a new genus *Kalmiopsis*. He had compared it with *Rhodothamnus Chamaecistus*, from



Figs. 67-74. *Rhodothamnus Leachianus*. 67. Vascular system in floral receptacle ×40; labels as in fig. 29. 68, 69. Young stamens ×8. 70, 71. Cross sections, respectively at a lower and a higher level, of a young anther, ×320. 72. Anther in preservative ×8. 73. Same, dried, ×8. 74. Fruit ×4.

which it differs in various characters, the one seemingly of generic significance being its possession of scale-like glands resembling those of *Rhododendron*. It now appears that the scales of *Kalmiopsis* are essentially different from those of *Rhododendron*. There is no occasion for keeping it separate from *Rhodothamnus*, which accordingly includes two species:

1. RHODOTHAMNUS CHAMAECISTUS Reichenbach in Mössler Handb. ed. 2, 1:688. 1827. *Rhododendron Chamaecistus* L. Sp. Pl. 392. 1753. Essentially glabrous (sepals ciliate, filaments pubescent below); leaves obscurely toothed. Flowers few in the axils of the upper leaves, corolla rotate, the lobes separate almost to the base, style long-exserted. Europe: eastern Alps. Report of this species in Siberia is based, according to Maximowicz, on misidentification of *Therorhodion Redowskianum*. Drude overlooked this information, and has been taken to task, for example, by Hegi (41, p. 1046) and Wilson (107).

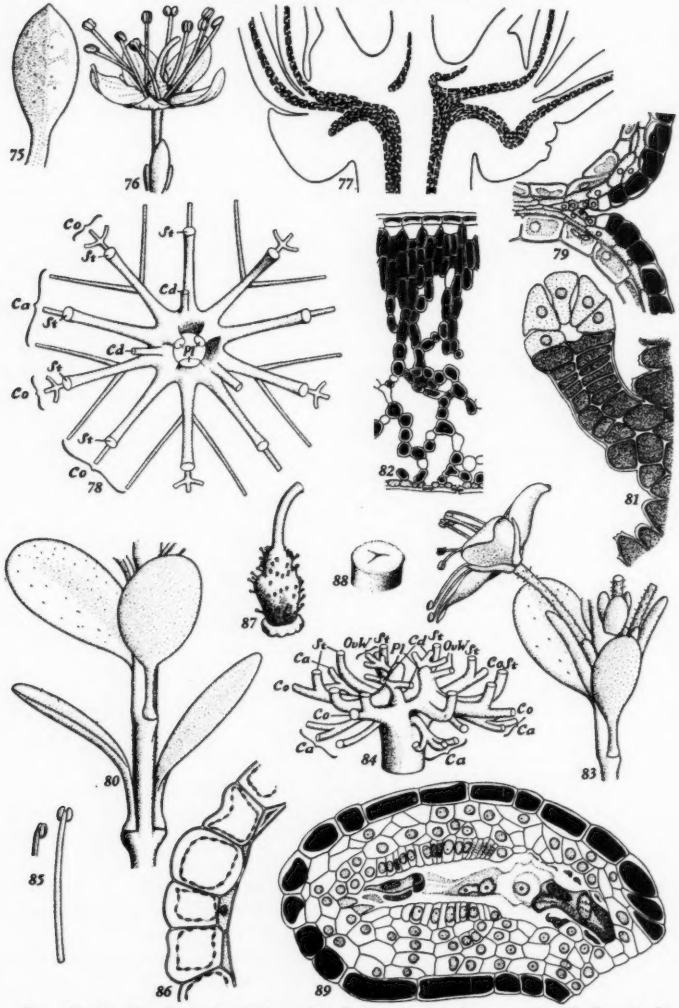
2. RHODOTHAMNUS LEACHIANUS (Henderson). *Rhododendron Leachianum* Henderson in Rhodora 33:205. 1931. *Kalmiopsis Leachiana* Rehder in Jour. Arnold Arb. 31:32. 1932. Beset with simple and glandular hairs, some of the latter being modified and scale-like. Flowers in terimnal racemes which, as the lower pedicels elongate, become corymbose. Corolla open-campanulate, sinuses between the lobes shallow. Style briefly exserted. Oregon: Curry County, summits of the Siskiyou Mountains; type from Horse Sign Butte, *Mr. and Mrs. J. R. Leach 2915* (in part), June 14, 1930.

Rhodothamnus Chamaecistus is known to me only by description. Although *R. Leachianus* grows within a few hundred miles of my place of work, I know it only by an excellent specimen in preservative furnished by the Arnold Arboretum.

The plants are low shrubs. They have repeately been described as of the aspect of minuscule rhododendrons. The stems show deviation from the anatomical characters set forth above as typical only in the feeble development of the layer of fibers of pericycle, an incomplete single layer of cells.

The leaves are 1-2 cm. long, broadly elliptic to obovate, briefly petioled, acute, rather thick. Anatomically, those of *R. Leachianus* (fig. 63) agree in most respects with those of *R. Chamaecistus* as described by Breitfeld. Both species have a moderately thick cuticle on both surfaces. The upper epidermis of *R. Chamaecistus* is said to consist of small cells with thick walls; I would describe that of *R. Leachianus* as consisting of large cells. In both species the palisade tissue is of two or three layers of moderately elongate cells, its total thickness about equalling that of the spongy tissue. Breitfeld described the veins as "*durchgehend*," i. e., as bordered above and below by flanges of fibers extending toward or to the epidermis. This is not true of *R. Leachianus*, which differs furthermore in the pubescence.

The pubescence of *R. Leachianus* is better developed upon the flowers than upon the vegetative parts. Simple hairs are sparse on the base of the corolla and the bases of the filaments, more abundant on the lower half of the ovary. Normal glandular hairs (fig. 64) are abundant on pedicels, outer surfaces of



Figs. 75-79. *Dendrium buxifolium*. 75. Leaf ×4. 76. Flower ×4. 77. Longitudinal section of floral receptacle ×40. 78. Vascular system in floral receptacle ×40; labels as in fig. 29. 79. Portion of cross section of young anther ×320.

Figs. 80-89. *Dendrium Lyoni*. 80. Stem and leaves ×4. 81. Gland of ovary ×320. 82. Cross section of leaf ×100. 83. Flower ×4. 84. Vascular system in floral receptacle ×40; labels as in fig. 29. 85. Stamen and anther ×8. 86. Portion of cross section of dehisced anther ×320. 87. Pistil ×8. 88. Stigma ×40. 89. Longitudinal section of ovule ×320.

sepals and petals, and ovaries. The scale-like glandular hairs (figs. 63, 64) are evidently a modification of the normal glandular hairs. The stalk is abbreviated, often to a single tier of cells; the head is laterally expanded, consisting of several tiers, each of several concentric cycles of cells. The head secretes a firm outer wall of some stain-resistant material. Then, as secretion proceeds, the cells shrivel away from the wall until they form a heavily staining amorphous mass at the end of the stalk (fig. 63).

The flowers are white to pink and exemplify perfectly the normal rhododendroid characters. Detailed description would be mere repetition.

The base of the receptacle is impressed and the main bundles of the calyx originate at nearly the same level as the petal bundles (fig. 67). All these bundles are recurved near their origin. The sepal laterals originate as branches of the petal bundles. The petalad stamen bundles are adnate for some distance to the petal bundles. The sepalad stamen bundles show some tendency toward adnation to the sepal bundles, and the carpel dorsals show some adnation to the petal and petalad stamen bundles.

The anthers of *R. Leachianus* (figs. 68-73) agree almost to the last detail with those of *R. Chamaecistus* as described by Artopoeus. The epidermis is in the lower part of approximately isodiametric cells, tanniniferous except in the shallow groove between the pollen sacs of each lobe. Here the epidermis is underlain by a column of resorption tissue (fig. 70). Near the summit, the epidermal cells are columnar; the groove between the pollen sacs is deep, and at the bottom of it the epidermal cells are of the character of resorption tissue (fig. 71). In this part of each lobe, the hypodermal cells on the side away from the groove become tanniniferous and thick-walled. The disappearance of the resorption tissue, together with the collapse of the adjacent cells, produces an open cleft in the upper part of the anther, and the tangential contraction of the columnar epidermal cells causes the cleft to gape widely.

The fruit (fig. 74) is a globular septicidal capsule (the valves becoming split at the summit); the seeds are minute, ellipsoid.

5. DENDRIUM Desvaux

There occurs, in the pine-barrens of New Jersey, a rhododendroid plant which, when brought to Europe about the beginning of the nineteenth century, was described under two different names, *Ledum buxifolium* Bergius and *Ledum thymifolium* Lamark. Persoon (76, p. 477) placed it in a distinct subgenus *Leiophyllum*, and Hedwig *filius* (40, p. 313) described *Leiophyllum* as a genus, without naming any species, but with sufficient description and reference to make it clear that it was to include particularly *Ledum thymifolium* Lamark. Evidently Hedwig's publication was obscure: when other authors decided that *Ledum buxifolium* is to be placed in a distinct genus, they published respectively *Dendrium buxifolium* Desvaux, *Ammyrsine buxifolia* Pursh, *Fischeria buxifolia* Swartz, and, finally, *Leiophyllum buxifolium* Elliott, with the generic name ascribed to Persoon, not to Hedwig f. Small (93) rejected

the name *Leiophyllum* on account of the priority of *Leiophyllum* Ehrhart. It has been pointed out by Barnhart (3), Fernald (31), and Camp (12), that *Leiophyllum* Ehrhart was published as a uninomial name for some plant or other, in effect as a Latin common name or nick-name. There is a passage in the rules (10) which uses Ehrhart's uninomials as specific examples of nomenclatorial nullities. Small's objection to *Leiophyllum* is of no standing. For my part, I reject *Leiophyllum* because it was not published in combination until after another name for the same genus (actually, several others) had been published with specific combinations. This is perhaps not warranted by the letter of the rules, but is a practical necessity in a system strictly of binomial names fixed by types. The botanists in congresses which declined to recognize the type system have recognized this necessity in an oblique way in three parallel cases in the present limited subfamily, by conserving *Rhodothamnus* as against *Adodendrum, Loiseleuria* as against *Chamaecistus,* and *Daboecia* as against *Boretta.* The type system being now accepted as an essential feature of botanical nomenclature, none of these accepted names requires conservation; but *Leiophyllum,* which acquired nomenclatorial status only with the publication of *Leiophyllum buxifolium,* is antedated by *Dendrium* Desvaux.

The genus includes, besides the type species, one other and one variety (cf. Camp, 12):

1. DENDRIUM BUXIFOLIUM Desvaux in Journ. de Bot. **1**:36. 1813. *Ledum buxifolium* Bergius in Acta Acad. Petrop. **1**(1):213. 1778; abundant other synonyms as above. Erect; leaves alternate, elliptic, obtuse; pedicels eglandular; style about twice as long as the ovary. New Jersey, coastal plains.

1a. **Dendrium buxifolium** var. **Hugeri** (Small) comb. nov. *Dendrium Hugeri* Small in Bull. Torrey Bot. Club. **28**:360. 1901. *Leiophyllum Hugeri* Schneider. *L. buxifolium* var. *Hugeri* Schneider. Pedicels glandular, style about as long as the ovary. Coastal plains, South and North Carolina and New Jersey. Camp gives reason for supposing this variety to be the primitive form among the representatives of the genus.

2. DENDRIUM LYONI (Sweet) Small in North Amer. Flora **29**:39. 1914. The description under *Ammyrsine* by Sweet is said to be very inadequate, and we have another specific epithet in *Ammyrsine prostrata* Loudon: Small gives a synonymy in which both epithets have been tried under three generic names, and *prostrata* furthermore as a varietal epithet under two species: to all of which may be added, no doubt, *Ledum Lyoni* Hort. ex Rehder in Bailey Std. Cycl. Hort. **4**:1833. 1916. Erect or prostrate, leaves for the most part opposite, broadly elliptic, rounded at apex; pedicels glandular; ovary contracted above, the style about equalling it. Tennessee and North Carolina in the mountains.

For anatomical study, I have flowering specimens, of *D. buxifolium* collected by Higinbotham in New Jersey, of *D. Lyoni* collected by Camp in the Great Smoky Mountains National Park in Tennessee.

The plants are shrubs, low or prostrate. Simple hairs occur on stems, petioles, pedices, and calyces; glandular hairs (fig. 81) occur sparsely on leaf blades, and on pedicels, calyces, and ovaries. Within the stems, the sheath of

fibers of pericycle is almost extinct, surviving only at a few points on the outer boundary of the phloem. The pith is small and consists entirely of small tanniniferous cells with thick pitted walls.

The numerous or crowded evergreen leaves are petioled, the blades about 5 mm. long, glabrous except for occasional glandular hairs. The thickness, about 500 μ, is exceptionally great (fig. 82). There is a heavy cuticle on both surfaces. The cells of the upper epidermis are notably large. The guard cells are exceptional in bearing prominent ridges at the inner openings of the pores as well as at the outer. The palisade tissue is of four or five layers of cells, occupying slightly less than half of the thickness of the leaf; the innermost palisade cells exhibit a transition to the spongy tissue. The veins, imbedded between normal paliside and spongy tissue, are in general of a thickness inconsiderable in comparison with that of the leaf. These observations agree with those of Breitfeld.

The flowers (figs. 76, 83), white to pink, less than 1 cm. in diameter, are few to several in a terminal raceme or corymb to the bracts of which there is a transition from the leaves. It will be recalled that they are choripetalous and pentamerous (the number of carpels reduced to three or two in all examples seen; according to Small there may sometimes be five); that the minute anthers open by slits as long as themselves; that the ovary is attenuate into the style, and that the stigma is not expanded. The filaments are glabrous.

The base of the receptacle is impressed (figs. 77, 78, 84); the main bundles of the sepals and the petal bundles arise at nearly the same level; the main bundles of the sepals are recurved in the proximal part of their course, while the petal bundles depart almost horizontally. In *D. buxifolium,* the lateral bundles of the sepals arise, as is usual in connection with the other features mentioned, as branches of the petal bundles; in *D. Lyoni* they arise variously, either as described, or from the main sepal bundles, or sometimes, no doubt, free in the tissue of the receptacle. The petalad stamen bundles are adnate through some distance to the petal bundles; the sepalad stamen bundles are separate from the sepal bundles. Above the departure of the stamen bundles, the vascular cylinder breaks up quite simply into alternating carpel dorsals and placental bundles, two or three of each. A few ovary wall bundles in addition to the carpel dorsals may arise as branches of the carpel dorsals or may run out through the septa from the placental bundles.

The epidermal cells of the anthers are tanniferous except at the bottom of the vertical groove on each lobe (fig. 79). The epidermal cells in this position, as well as a few adjacent hypodermal cells, are distinguished by small size and heavily staining contents; I interpret them as resorption tissue, though the usual granular appearance is not evident. Disappearance of these cells makes a narrow slit in the anther wall, and contraction of the remaining epidermal cells causes this to gape widely. The endothecium persists to some extent (fig. 86), but the cell walls are not thickened to form a rigid support for the contracting cells.

My material is without fruit or seeds.

6. DIPLARCHE Hooker f. et Thomson

The original description of *Diplarche* tells us that this and *Maddenia*, described with it, "are two of the most remarkable new genera that have hitherto presented themselves to us during the examination of our Indian Herbarium. . . ." It is exceptional among Rhododendroideae in the definitely serrate leaves, and among all Bicornes in the insertion of the stamens. Those of the sepalad whorl are epipetalously inserted high in the corolla: those of the petalad whorl may also be epipetalous, but at a lower level, or they may be free of the corolla. The area of *Diplarche* is distant and almost inaccessible. Fortunately, the original description, from which I draw most of the following account, was detailed, careful, and well illustrated.

From prostrate stems grow erect densely leafy shoots a span high. The leaves are linear, less than 1 cm. long, sessile, serrate, glabrous, shining, with about one-third of the width occupied by a midrib which is prominent on both sides; when they fall, they leave the stem densely covered with scars. From upper leaves there is a transition to bracts, somewhat shorter and more strongly serrate, the teeth tipped with hairs which are sometimes capitate. There is a flower sessile in the axil of each bract, embraced between a pair of bractlets resembling the bracts. Sepals five, separate, strongly serrate. Corolla tube cylindrical, as long as the sepals; limb spreading, about 5 mm. in diameter, divided into five suborbicular lobes. Stamens inserted as described above, filament perhaps 1 mm. long, anther 0.3 mm. long, attached at the summit, dehiscing by slits from top to bottom and gaping widely. Ovary globular, five-lobed; style brief; stigma broadly capitate, with five lobes: the figures appear to show a collar around them. In fruit, the pedicels elongate but slightly. "The ripe capsule appears to have two integuments, the outer coriaceous coat of each valve separating from the inner or more crustaceous one, whose margins alone are inflexed"; "the dorsal portion of the valves breaking away from the septa, which remain attached to the axis of the capsule as thin scarious membranes." Seeds numerous, elongate-obovoid, tailless.

There are two known species, both collected by J. D. Hooker in the Himalayas of Sikkim, 1848-1849:

1. DIPLARCHE MULTIFLORA Hooker f. et Thomson in Hooke's Jour. Bot. 6:383. 1854. Branchlets glandular-pubescent, leaves 5-8 mm. long, flowers on each shoot 8-20, subcapitate; in fruit the peduncle and rachis of the inflorescence become greatly elongate. By collections of Rock and Forrest, this species is now known to occur in northwestern Yunnan and adjacent Tibet: apparently it is common among rocks above timberline.

2. DIPLARCHE PAUCIFLORA Hooker f. et Thomson l. c. Branchlets subglabrous, leaves 2-5 mm. long, flowers 2-6 near the end of each branchlet, the peduncle and rachis not elongating in fruit. Known apparently only by the original collection.

7. KALMIA L.

Kalmia, named by Linnaeus for his student, the explorer Peter Kalm, was

represented in the *Species Plantarum* by *K. latifolia* and *K. angustifolia*. There have been few nomenclatorial complications in this group: the only generic synonym is *Kalmiella*, proposed by Small (94) as a segregate. The genus is confined to North America (and Cuba). The original species are fairly large shrubs and are called mountain laurels. They are known to poison sheep and cattle. *K. latifolia* is the state flower of Connecticut.

The following synopsis of the species is essentially a radical rearrangement of Small's presentation (95):

I. Plants beset with bristles. Shrubs of moderate size, leaves alternate, rarely more than 1 cm. long. Southeastern United States and Cuba. Genus *Kalmiella* Small.

1. KALMIA HIRSUTA Walt. Stems, margins of leaves, and pedicels beset with bristles. Leaves ovate, oblong, or lanceolate, glabrous below. Flowers axillary along the branches, to 15 mm. broad. Virginia to Florida and Alabama.

2. KALMIA ERICOIDES C. Wright ex Griesbach. Stems and pedicels glandular-bristly. Leaves revolute, essentially glabrous. Flowers in the axils of the more or less reduced upper leaves, to 15 mm. broad. Western Cuba.

3. **Kalmia aggregata** (Small) comb. nov. *Kalmiella aggregata* Small in North Amer. Flora 29:54. 1914. Stems and pedicels with bristles and simple hairs, leaves revolute, beset with simple hairs especially below, flowers in the axils of the more or less reduced upper leaves, to 2 cm. across, fllaments glabrous. Isle of Pines.

II. Plants without bristles but with more or less abundant glandular hairs. Large or moderately large shrubs, flowers in bracted umbel-like corymbs. Eastern United States and Canada.

A. Large shrubs, corymbs terminal and in the axils of the upper leaves, glandular hairs abundant on stem and flowers.

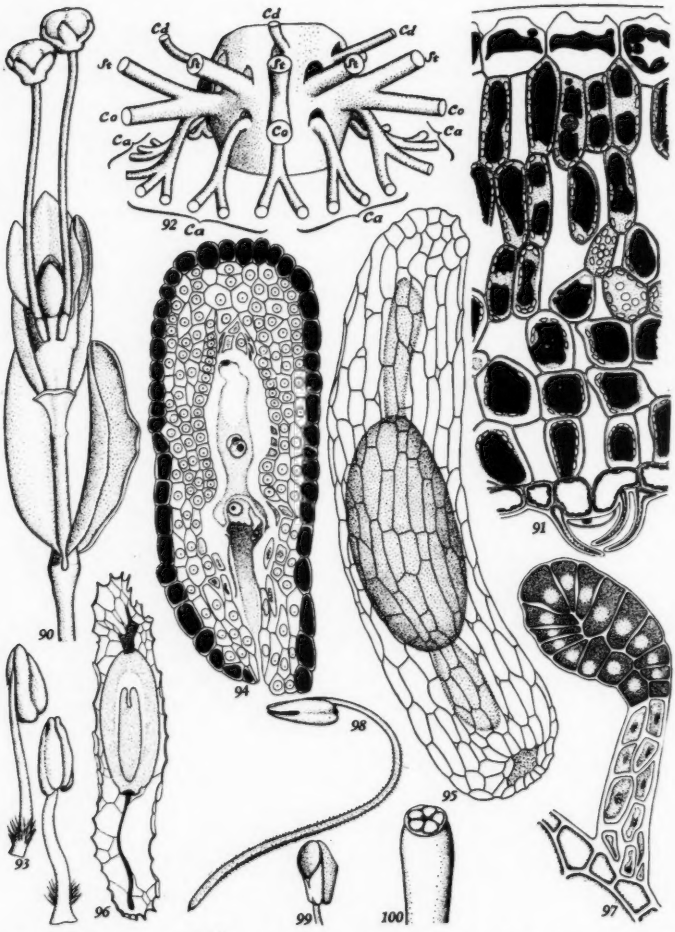
4. KALMIA LATIFOLIA L. Sp. Pl. 391. 1753. Leaves alternate or opposite, elliptic, to 8 cm. long, glabrescent or glabrous. Flowers to 2.5 cm. across. Eastern Canada to Louisiana.

B. Shrubs of moderate size, corymbs in the axils of leaves (terminal bud continuing the stem), glandular hairs confined to the flowers.

5. KALMIA CUNEATA Michaux Fl. Bor. Am. 1:257. 1803. Low shrubs, stems, lower surfaces of leaves, and pedicels with simple hairs, leaves obovate to cuneate, mucronate, to 5 cm. long; flowers to 1.5 cm. across, ovary with glandular hairs. Lowlands of North and South Carolina.

6. KALMIA CAROLINA Small Fl. S. E. U. S. 886. 1903. Leaves, stems, pedicels and ovary with simple hairs; ovary and sometimes calyx with glandular hairs. Leaves elliptic to oblong, to 9 cm. long, obtuse to mucronulate, flowers to 8 mm. across, style sometimes pubescent. Virginia to South Carolina.

7. KALMIA ANGUSTIFOLIA L. Sp. Pl. 391. 1753. Stems and leaves glabrous or glabrescent. Leaves mostly opposite, oblong to lanceolate. Flowers about 1



Figs. 90-96. *Kalmia polifolia* var. *microphylla*. 90. Shoot with fruits ×1.6. 91. Cross section of leaf ×320. 92. Vascular system in floral receptacle ×40; labels as in fig. 29. 93. Stamens ×8. 94. Longitudinal section of ovule ×320. 95. Seed ×80. 96. Longitudinal section of seed ×40.

Figs. 97-100. *Kalmia latifolia*. 97. Gland of ovary ×320. 98. Stamen in preservative ×8. 99. Anther, dried, ×8. 100. Stigma ×8.

cm. across, pedicels, calyx, ovary, and corolla more or less beset with glandular hairs. Northern Canada to Georgia.

III. Plants without bristles or glandular hairs; shrubs of moderate size or low, stems glabrous or with simple hairs, leaves normally opposite, strongly simple-pubescent below; flowers in the axils of upper leaves of the year.

8. KALMIA POLIFOLIA Wangenh. *K. glauca* Aiton. Shrubs of moderate size, leaves strongly revolute, to 3 cm. long, flowers to 1.5 cm. wide. Northern Canada to New Jersey, Pennsylvania, and Minnesota.

8a. KALMIA POLIFOLIA var. MICROPHYLLA Rehder in Bailey Cycl. Am. Hort. 2:854. 1900. *K. glauca* var. *microphylla* Hooker Fl. Bor. Am. 2:41. 1834. *K. microphylla* Heller. *K. occidentalis* Small in North Amer. Flora 29: 53. 1914. Lower than the species, leaves and flowers generally smaller, leaves often less strongly revolute. Sizes of plants and of parts and degree of revolution of leaves vary independently of one another in this group; if one distinguishes species by them, he will discover not only the two which Hellar and Small have proposed, but several others. This name may be used for all of the western material, Alaska and Yukon to California and Colorado, confined southward to high altitudes.

For anatomical study I have material of *K. polifolia* var. *microphylla* collected in Yosemite National Park by Camp, on Mount Lassen by myself, and near Juneau by the Juneau Botanical Club; and buds and flowers of *K. latifolia* collected by Camp in New York and Ohio.

The stems of *K. polifolia* var. *microphylla* include an exceedingly thin and fragmentary sheath of fibers of pricycle.

The leaves of this variety (fig. 91) are about 250 μ thick, with epidermal cells large above, small below, on both sides with a thick cuticle. On the lower side there are abundant slender simple hairs. The palisade is of two or three layers of cells, occupying about half of the thickness of the leaf; the cells are not extremely slender, and there is a transition to the not very different spongy tissue. The veins are imbedded between palisade and spongy tissue, lacking prominent flages of fibers above and below.

Breitfeld sectioned leaves of *K. glauca* (i. e., *K. polifolia*), *K. angustifolia, K. latifolia,* and *K. hirsuta.* He found each to exhibit marked specific characters. As to the first, his account differs from the one just given in that he finds only two layers of palisade cells, and also (according to my supposition stated previously in the general part) in misinterpretation of some of the simple hairs. He notes a resemblance between this species and *Daboecia, Loiseleuria,* and *Bryanthus* (i. e., *Phyllodoce*). He compares *K. angustifolia* with *Rhodothamnus* and *Leiophyllum:* this is to say that the leaf is distinctly thicker, the epidermal cells small and thick-walled and the cuticle thick on both sides. I do not find a statement as to whether the veins are *"durchgehend,"* as in *Rhodothamnus Chamaecistus,* or not, as in *Dendrium:* I take it that they are not. The statement that *K. latifolia* "zeigt die Epidermiszellen der Section Azalea und stimmt sonst völlig mit *Rhodothamnus Chamaecistus* überein" means that

this species is similar except for larger, thinner-walled cells in the upper epidermis. *K. hirsuta* is said to agree, in most respects, with *Azalea:* the leaf is thin, presumably with a single layer of palisade cells; the upper epidermis is of large cells, the lower of small ones, cuticle thin on both sides, both bristles and simple hairs present; the only differences are the relatively fewer bristles and the absence of flanges of fibers above and below the veins.

Among reproductive structures, the corolla particularly requires description. It is white to pink, red, or purple, and of peculiar shape: a brief and broadly cylindrical tube gives way to a flaring, almost rotate limb upon which the lobes may be spreading or erect. At the level of the bases of the lobes there are ten outpocketings in the planes of the lobes and alternating with them. In bud, these outpocketings or sacs are erect; the filaments, elongating not long before anthesis, carry the anthers into them. When the corolla opens, the anthers are carried away from the axis of the flower, the elastic filaments becoming curved. At any disturbance of the flower, the anthers are released from the sacs and flung upward, discharging the pollen centrifugally. This pollen-discharging mechanism is the distinctive character of the genus.

The vascular system in the floral receptacle (fig. 92) agrees with that of the genera already described in which the base of the receptacle is impressed. The main bundles of the calyx originate not far below the petal bundles and are reflexed in the proximal part of their course. The sepal lateral bundles arise as branches of the petal bundles: in this case, adjacent sepal laterals are coalescent to some distance from their origin. The petalad stamen bundles are adnate to the petal bundles; the sepalad stamen bundles are not united with others. There are gaps extending a considerable distance above the combined petal and petalad stamen bundles and the carpel dorsals arise inconspicuously beside them.

The structure of the anther (figs. 93, 98, 99) has been described by Artopoeus, described and figured by Matthews and Knox. It is quite as in *Rhodothamnus* and *Phyllodoce*.

Peltrisot based his well-illustrated account of the development of seeds on material of *K. glauca, K. angustifolia, K. latifolia,* and *K. myrtifolia* (a horticultural variant of *K. latifolia*). I have not seen stages between the ovule (fig. 94) and the ripe seed (figs. 95, 96). These conform to his account. Internal integumental cells remain present within the epidermis as empty spaces, particularly at the ends of the seeds, which are extended as tails or wings. They make the seeds light, and I note openings from the outer air in among them at the angles between the epidermal cells.

8. PHYLLODOCE Salisbury

One species of *Phyllodoce* occurs in arctic Europe, and appeared in the *Species Plantarum* as *Andromeda caerulea*. The flowers not being blue, Pallas renamed it *A. taxifolia;* and when Salisbury recognized it as generically distinct, he used the later specific epithet. Both this genus and *Menziesia* include species with urceolate corollas, and older authors were disposed to include this genus

in *Menziesia*. David Don ended this confusion by pointing out the fact that *Menziesia* has strobiloid winter buds. Asa Gray (35) introduced confusion with another genus, reducing *Phyllodoce* to *Bryanthus*. A stable understanding of the group dates from Maximowicz (67).

The classification appears to be as follows (Rehder, 81; Stoker, 102):

I. The species.

A. Corolla campanulate; calyx and corolla glabrous.
1. Lobes of the corolla shorter than the tube.

1. PHYLLODOCE EMPETRIFORMIS D. Don in Edinburgh New Phil. Jour. 17:160. 1834. *Menziesia empetriformis* Smith. *Menziesia Grahamii* Hooker Fl. Bor. Am. 2:40. 1834. *Phyllodoce Grahamii* Pursh in Trans. Am. Phil. Soc. n. s. 8:269. 1843. *Bryanthus empetriformis* Gray in Proc. Am. Acad. 7:367. 1868. Leaves to 15 mm. long; corolla pink, to 9 mm. long. Yukon to the Siskiyou Mountains and Mount Shasta in California.

2. PHYLLODOCE NIPPONICA Makino in Bot. Mag. Tokyo 19:131. 1905. Leaves to 15 mm. long, corolla rose (according to the original description; white according to Stoker), to 9 mm. long. Japan: Hokkaido and Honshu.

2a. PHYLLODOCE NIPPONICA var. AMABILIS Stoker. *P. amabilis* Stapf. *P. empetriformis* var. *amabilis* Rehder in Bailey Std. Cycl. Hort. 5:2607. 1916. A white-flowered form discovered in cultivation at Kew.

2. Lobes of the corolla as long as the tube.

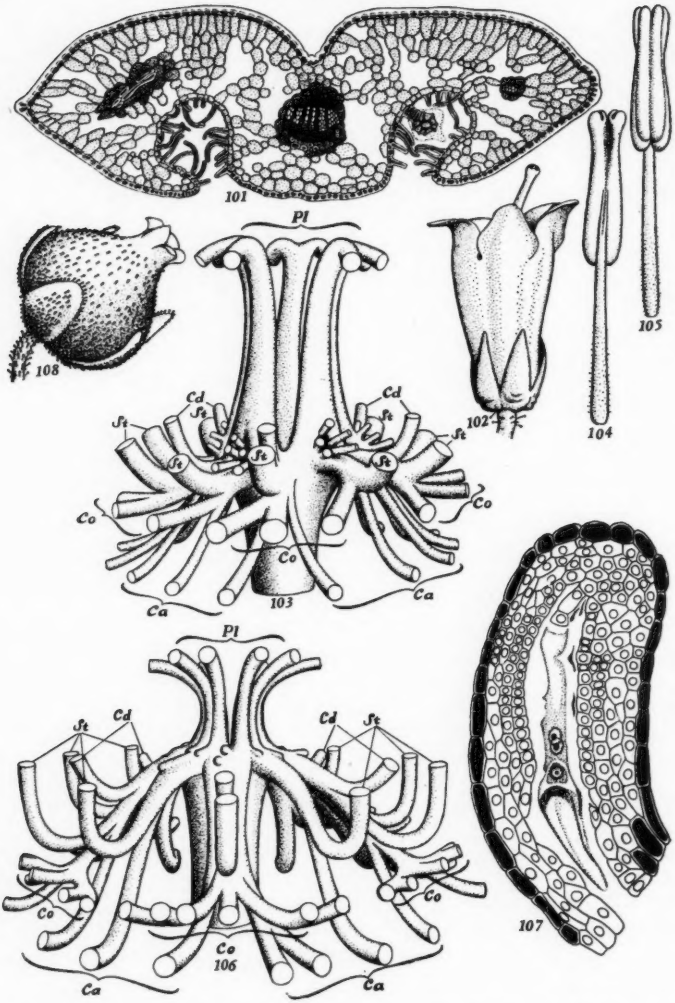
3. PHYLLODOCE BREWERI Maximowicz in Mem. Acad. Sci. St. Pétersbourg sér. 7, vol. 16, no. 9: 5. 1870. *Bryanthus Breweri* Gray in Proc. Am. Acad. 7:367. 1868. Leaves to 21 mm. long, corolla broadly campanulate, red, to 8 mm. long. California: Sierra Nevada, also San Bernardino Mountains. Jepson (51) points out that the areas of *P. empetriformis* and *P. Breweri* are mutually exclusive.

B. Corolla urceolate, calyx glandular.
1. Corolla glabrous, filaments glabrous or nearly so.

4. PHYLLODOCE CAERULEA Babington. *Andromeda caerulea* L. Sp. Pl. 393. 1753. *Andromeda taxifolia* Pallas Fl. Ross. 2:54. 1788. *Phyllodoce taxifolia* Salisbury Parad. Lond. t. 36. 1806. *Menziesia caerulea* Swartz. *Bryanthus taxifolius* Gray in Proc. Am. Acad. 7:368. 1868. Leaves to 9 mm. long, flowers red to purple, to 8 mm. long. Mountain tops in New England; Quebec, Greenland, Iceland, Scotland, and eastward to Kamchatka; apparently not in western North America.

5. PHYLLODOCE ALPINA Koidzumi. Leaves to 8 mm. long, corolla 6 mm. long, bluish. Japan.

6. PHYLLODOCE ALEUTICA Heller in Muhlenbergia 1:1. 1900. *Menziesia aleutica* Sprengel Syst. 2:202. 1825. *Phyllodoce Pallasiana* D. Don in Edinburgh New Phil. Jour. 17:159. 1834. *Bryanthus aleuticus* Gray in Proc. Am.



Figs. 101-105. *Phyllodoce empetriformis*. 101. Cross section of leaf ×80. 102. Flower ×4. 103. Vascular system in floral receptacle ×40; labels as in fig. 29. 104, 105. Stamens ×8.

Figs. 106, 107. *Phyllodoce Breweri*. 106. Vascular system in floral receptacle ×40; labels as in fig. 29. 107. Longitudinal section of ovule ×320.

Fig. 108. *Phyllodoce glanduliflora*. Flower ×8.

Acad. 7:368. 1868. Leaves to 9 mm. long, flowers yellow (to white ?), to 7 mm. long. Alaska, Kamchatka.

2. Corolla glandular-pubescent, filaments pubescent.

7. PHYLLODOCE GLANDULIFLORA Coville. *Menziesia glanduliflora* Hooker Fl. Bor. Am. 2:40. 1834. *Bryanthus glanduliflorus* Gray in Proc. Am. Acad. 7:368. 1868. Leaves to 14 mm. long; corolla yellow, to 8 mm. long. Alaska and Yukon to Montana and Oregon.

II. The hybrids.

PHYLLODOCE INTERMEDIA Rydberg in Mem. New York Bot. Gard. 1:298. 1900. *Menziesia intermedia* Hooker Fl. Bor. Am. 2:40. 1834. This name represents hybrids between *P. empetriformis* and *P. glanduliflora*. As Camp (13) points out, these will show, after the first generation, every possible combination of characters, and it is not feasible to equip all of these with names. Accordingly, he reduces to this *P. hybrida* Rydberg in Mem. New York Bot. Gard. 1:298. 1901, and *P. pseudoempetriformis* Stoker in New Flora and Silva 12:40. 1939.

PHYLLODOCE TSUGAEFOLIA Nakai has never been published in proper form. From Stoker's interpretation of its characters, it appears that it may represent hybrids between *N. nipponica* and *P. alpina*.

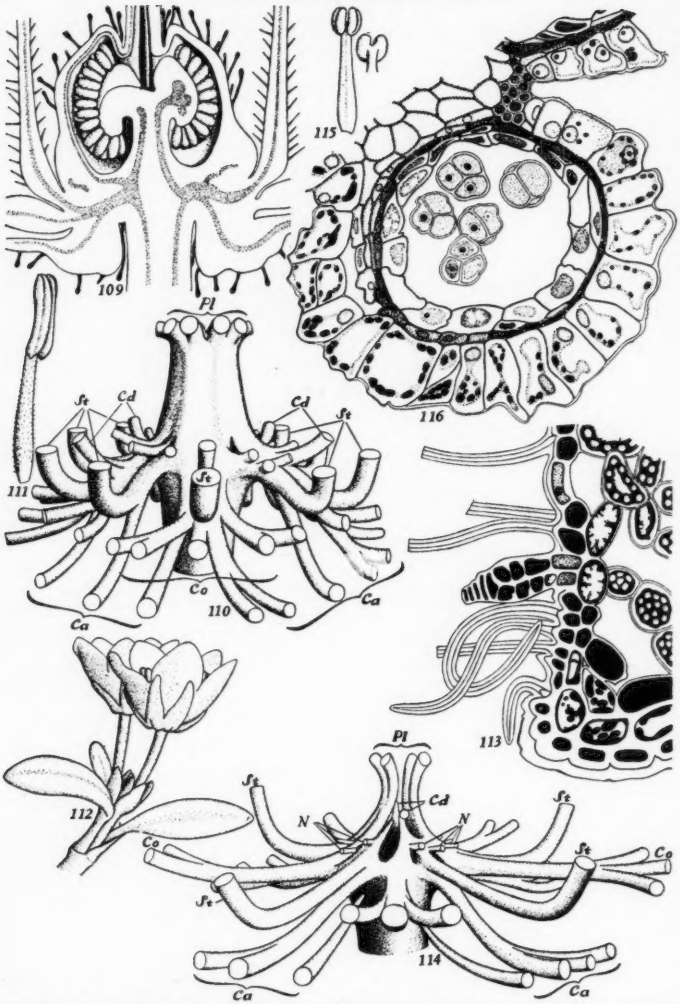
Where *P. caerulea* and *P. aleutica* are in contact, they are said to hybridize freely; the hybrids have apparently not been honored with a name.

PHYLLODOCE ERECTA Drude in Engler et Prantl Nat. Pflanzenfam. 4(1): 39. 1889. *Bryanthus erectus* Lindley. A hybrid of *Phyllodoce empetriformis* and *Rhodothamnus Chamaecistus* which originated in a nursery in Scotland about 1845. Leaves as in *Phyllodoce;* flowers large, pink, saucer-shaped.

For anatomical study, I have flowering material of *Phyllodoce Breweri* collected by Mr. H. M. Skidmore at Wright's Lake in the Sierra Nevada and by myself on Mount Lassen; of *P. empetriformis,* collected on Mount Rainier by Camp and by myself; and of *P. glanduliflora,* collected on Mount Rainier by Camp and near Juneau by the Juneau Botanical Club.

The plants are low shrubs with a pubescence of simple and glandular hairs. Within the stem, the cortex is a rather thin layer, and the layer of fibers of pericycle which forms its inner boundary is a nearly complete single layer of cells.

The heath-like leaves are crowded, closely revolute, the margins approaching the midrib below and producing the appearance of a doubly grooved lower surface. Those of the three species studied are essentially identical in anatomical characters (fig. 101). The total thickness approaches 400 μ; if we imagine the lamina unrolled, its greatest thickness, near the midrib, would be about 200 μ. The upper epidermis, and the lower epidermis of the midrib, with which it is almost in contact, are of small thick-walled tanniniferous cells with a very



Figs. 109-111. *Phyllodoce glanduliflora*. 109. Longitudinal section of floral receptacle and ovary ×20. 110. Vascular system in floral receptacle ×40; labels as in fig. 29. 111. Stamen ×8.

Figs. 112-116. *Loiseleuria procumbens*. 112. Summit of shoot with flowers ×4. 113. Portion of cross section of leaf ×320. 114. Vascular system in floral receptacle ×40; labels as in fig. 29. 115. Stamen and anther ×8. 116. Portion of cross section of young anther ×320.

heavy cuticle. Breitfeld saw this in these species, which he treated as belonging to *Bryanthus;* in *P. taxifolia* and *P. aleutica,* which he recognized as belonging to *Phyllodoce,* he found a thin cuticle. The lower epidermis, lining the grooves, is of smaller cells with a thin cuticle. It is densely beset with simple hairs and bears a few glandular hairs. The palisade tissue is of two or three layers (Breitfeld found three or four) of slightly elongate cells; these follow the thick-walled epidermis around to the margins of the grooves, forming a thinner layer as they approach it, making up everywhere about half of the true thickness of the leaf. Because of the structure of the epidermis and the palisade tissue, I cannot agree with Stoker, who holds that the lateral extremities of the leaf are the true margins, and that it is not revolute but gives a false appearance of this condition by a differentiation of the lower surface. The veins are imbedded in the mesophyll; they are bordered by fibers above and below, but these do not form massive wings or flanges.

The flowers (figs. 102, 108) are borne in the axils of leaves of the year. Their general characters are altogether those typical of the group.

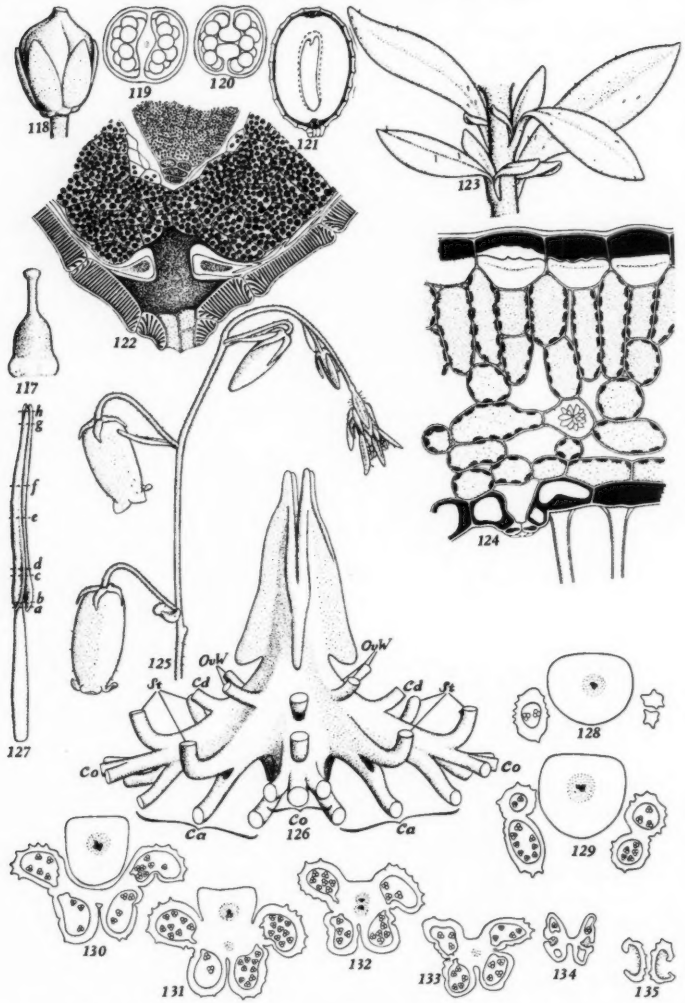
The floral receptacle is deeply impressed at the base, and the vascular system within it (figs. 103, 106, 109, 110) exhibits markedly the features associated with this condition. The main bundles of the sepals and the petal bundles arise nearly at the same level, and both sets of bundles are recurved through the proximal part of their courses. The sepal lateral bundles originate as branches of the petal bundles. The petalad stamen bundles are adnate through a considerable distance to the petal bundles; the sepalad stamen bundles are adnate to the main bundles of the sepals, and the carpel dorsals to the combined petal and petalad stamen bundles. Above the departure of the ten main bundles, which, with their branches, have just been described, a number of obscure bundles run out into the nectary and the remainder of the vascular tissue draws together and ascends the central column of the ovary.

In all essentials of structure and behavior, the anthers are quite as in *Rhodothamnus* and *Kalmia.* They have been described and figured by Artopoeus and by Matthews and Knox.

The ovule (fig. 107) is moderately elongate. I have no material of further stages for microscopic examination; the seeds of herbarium specimens are of about the same shape as the ovules and show no traces of wings or tails. Peltrisot found scant bodies of internal integumental cells remaining in the ends.

9. LOISELEURIA Desvaux

All authorities agree that the sixth species of *Azalea* in the *Species Plantarum,* namely *A. procumbens,* is to be placed in a genus by itself. Postponing discussion of the proposition maintained by Rehder (82), with abundant earlier authority, that this is the true *Azalea,* I account for it under the oldest binomial name given to it in a distinct genus:



Figs. 117-122. *Loiseleuria procumbens*. 117. Pistil ×8. 118. Fruit ×4. 119, 120. Cross sections, respectively at a lower and a higher level, of a fruit, ×4. 121. Longitudinal section of a seed ×40. 122. Micropylar portion of same ×320.

Figs. 123-135. *Daboecia cantabrica*. 123. Stem and leaves ×4. 124. Cross section of a leaf ×320. 125. Raceme ×1.6. 126. Vascular system in floral receptacle ×40; labels as in fig. 29. 127. Stamen ×8. 128-135. Cross sections of the anther at the levels marked *a* to *h* in fig. 127, ×40.

LOISELEURIA PROCUMBENS (L.) Desvaux in Jour. de Bot. 1:35. 1813. Circumpolar in the arctic region; European Alps; south in North America to the White Mountains of New Hampshire.

For anatomical study, I have a flowering specimen collected near Juneau by the Juneau Botanical Club.

The plant is a low or prostrate shrub with a pubescence of simple and glandular hairs, the latter few and frequently abortive. In the stem, the pericycle is not differentiated. The pith consists entirely of small tanniniferous cells with thick walls.

The leaves are mostly opposite, briefly petioled, less than 1 cm. long, broadly elliptic, obtuse (fig. 112). They are revolute, but less strongly so than those of *Phyllodoce*. The thickness of the lamina is about 400 μ. The epidermis is of small thick-walled cells (fig. 113) and there is a heavy cuticle above and on the lower surface of the midrib. The lower epidermis, lining the two cavities on the lower side, is densely beset with simple hairs which are elongate and curved. Among these there are other trichomes which are evidently reduced glandular hairs: a stalk, usually biseriate, of thick-walled tanniniferous cell ends, not in a gland, but in a few flattened cells of moribund appearance. The stomatal pores are bounded at the outer openings by prominent ridges, at the inner openings by obscure ones. The palisade tissue is of slightly elongate cells; it occupies about half of the thickness of the leaf, consisting of four or more layers near the midrib and tapering off to one near the margin. Near the margins and on the lower surface of the midrib, and extending a slight distance under each edge of the lower epidermis, there is a hypodermis. The veins are imbedded between palisade tissue and spongy tissue. Many of these data have already been recorded by Breitfeld.

The flowers are borne in the axils of the more or less reduced upper leaves on pedicels less than 1 cm. long. The base of the receptacle is impressed. The open-campanulate corolla, with ovate and rounded or apicualte lobes as long as the tube, is white to red, less than 1 cm. in diameter. The stamens are five, opposite the sepals, with flattened filaments; the isodiametric strongly bilobed anthers open by slits as long as themselves. The pistil is of two or three carpels, the ovary attenuate into the style. The epidermis of the flowers part—sepals, petals, filaments, and pistils—is notably papillose. It bears a thin and markedly striate cuticle.

In connection with the impressed base of the receptacle, the ten main bundles of the perianth depart from the stele at nearly the same level and are recurved through the proximal part of their courses (fig. 114). The sepal lateral bundles may originate from the main sepal bundles; or from the petal bundles; or free in the tissue of the receptacle. The stamen bundles arise close above, but scarcely united with, the main sepal bundles. There depart from the stele, at about the same level as the stamen bundles, random obscure bundles supplying the nectary. The remainder of the vascular tissue becomes organized,

ordinarily, as six bundles, being two carpel dorsals and four placental bundles.

Each lobe of the anther is marked by a deep vertical groove extending the entire height of the lobe on the inner-lateral surface. In this groove there is, in the young anther, an epidermal and hypodermal column of resorption tissue; the epidermal cells elsewhere are somewhat columnar and somewhat tanniniferous. There is no thick-walled endothecium (fig. 116). Dehiscence involves the disappearance of the resorption tissue, the collapse of the tapetum, of the septum between the pollen sacs, and of the internal wall cells, and the lateral contraction of the epidermal cells. Artopoeus saw these anthers much as I have.

The ovules and seeds (figs. 121, 122) are subglobular; Peltrisot saw these, and also intermediate developmental stages. The seeds are yellow, about 0.5 mm. long, notable anatomically for the great thickening of the inner and lateral cell walls, traversed by slender channels, of the epidermal cells. In the dehiscence of the fruit, the two or three valves of the capsule become split at the summit.

10. BRYANTHUS D. Don

The name *Bryanthus* was published as that of a genus in Gmelin's *Flora Sibirica*. The nomenclature of this work is not binomial, and as there was no discrimination of species under *Bryanthus*, the name was allowed to stand by itself. The younger Linnaeus created for the plant in question the combination *Andromeda bryantha*. The plant being no *Andromeda*, his successors tried it in *Erica* and *Menziesia*, which also it is not, and finally David Don resurrected Gmelin's genus to include it. The epithet *bryantha* is not grammatically identical with the name *Bryanthus;* it is an adjective; but it cannot be placed after the generic name without creating a repeating binomial. Accordingly, Don introduced a new specific epithet, making the combination *Bryanthus Gmelini*. It is an anomaly that the type species of a genus named *by* Gmelin should be named *for* Gmelin. The anomaly seemed to be eliminated by the publication by Nakai of the combination *Bryanthus musciformis*, with reference of the epithet to Poiret. Poiret's pertinent words (78) are as follows: "7. Andromède musciforme, no. 7. *Andromeda briantha*. Linn." Here *musciforme* is the specific epithet in a French common name, translating the scientific name; it is of no nomenclatorial status, and Don's combination must stand. The true escape from the anomaly is by holding that Gmelin's authorship of the name in a work not observing binomial nomenclature is of no nomenclatorial status, and that D. Don is the author of the genus. The only species is the original one:

BRYANTHUS GMELINI D. Don in Edinburgh New Phil. Jour. 17:160. 1834. *Bryanthus* Gmelin Fl. Sibir. 4:132. 1769. *Andromeda bryantha* L. f. Mant. 238. 1771. *Erica bryantha* Thunberg. *Menziesia bryantha* Swartz. *Bryanthus musciformis* Nakai. Ohotsk Coast, Kamchatka, Hokkaido.

This low or prostrate shrub has spirally crowded linear spatulate leaves about 3 mm. long. They have a ridge along the midrib above, a deep groove beneath, a row of gland-tipped bristles along each margin (I suppose that the bristle-bearing edges are the false margins of a strongly revolute leaf, and that the true margins are the sides of the groove). The inflorescence is a raceme perhaps 2 cm. long, terminal on the growth of the year and bearing perhaps half a dozen flowers. The flowers are pedicellate, in the axils of scale-like bracts, without bractlets; regular, hypogynous, sympetalous, tetramerous; corolla rotate, about 3 mm. in diameter, pink, the rotund lobes much longer than the tube. Stamens eight, anthers opening by lengthwise slits. Pistils of four carpels. The stems and inflorescences bear simple and gladular hairs. Maximowicz (67) insists that the tetramerous condition is normal; it is probable that there is some variation.

No material for anatomical study has been available.

11. LEDOTHAMNUS Meissner

The type collection of *Ledothamnus* is cited as follows: "*Habitat in Guyana anglica, m. Dec.: Schomburgk n. 1548.; in Brasilia boreali quaerenda.*" Meissner's expectation of finding this genus in Brazil is unfulfilled; its only known locality, aside from Roraima, is Mount Auyan-Tepui in Venezuela. Three species and three varieties are based on specimens from these two small areas.

The plants are low shrubs, with the leaves whorled, often crowded, to 1 cm. long, oblong, in cross section triangular, with one of the surfaces directed upward and a deep groove in the downward angle. Simple hairs, bristles, and glandular hairs are present, variously distributed in different races; the leaves are usually ciliate with rather distant bristles or glandular bristles on the edges of the upper surface (these, it is presumed, are false margins, the true ones being the sides of the dorsal groove). The flowers are red, solitary and terminal or few in the highest leaf axils, pedicellate or sessile, regular, hypogynous, choripetalous, 5-, 6-, or 7-merous, open-campanulate to bowl-shaped, to 2.5 or 3 cm. wide. Filaments glabrous, anthers elongate, opening by slits nearly as long. Carpels as many as the petals; ovary globular, papillose; style columnar, straight, glabrous; stigma capitate; fruit a septicidal capsule.

The known races are classified as follows:

I. Flowers pedicellate, stamens twice as many as the petals, anthers about as long as the filaments.

A. Bristles of leaf-margins, pedicels, and calyces gland-tipped.

1. LEDOTHAMNUS GUYANENSIS Meissner in Martius Fl. Bras. 7:171. 1863. Young leaves beset with simple hairs, these persistent on the midrib. Roraima.

1a. LEDOTHAMNUS GUYANENSIS var. NITIDUS A. C. Smith in Brittonia 3:184. 1939. Leaves entirely glabrous. Auyan-Tepui.

B. Bristles not gland-tipped, or gland-tipped only on pedicels.

2. LEDOTHAMNUS TATEI A. C. Smith in Brittonia 3:184. 1939. Leaves glabrous except the ciliate margins. Auyan-Tepui.

Figs. 136-140. *Daboecia cantabrica*. 136. Ovary ×4. 137. Longitudinal section of ovule ×320. 138. Fruit ×4. 139. Longitudinal section of seed ×40. 140. Micropylar portion of same ×320.

Figs. 141-146. *Menziesia ferruginea*. 141. Simple hair of base of filament ×320. 142. Glandular hair of pedicel ×320. 143. Portion of cross section of stem ×320. *fp*, fibers of pericycle; *c*, cork; *p*, phloem; *x*, xylem. 144. Cross section of leaf ×320. 145. Tip of stem with floral and foliar winter buds. 146. Flower ×4.

2a. LEDOTHAMNUS TATEI var. PUBERULUS A. C. Smith in Brittonia 3: 185. 1939. Surfaces of the young leaves densely pubescent with simple hairs. Auyan-Tepui.

II. Flowers sessile or subsessile, stamens as many as the petals and alternate with them, filaments three to five times as long as the anthers.

3. LEDOTHAMNUS SESSILIFLORUS N. E. Brown in Trans. Linn. Soc. Bot. 6:45. 1901. *Ledothamnus guyanensis* var. *minor* Oliver. Marginal bristles of the leaves eglandular, surfaces puberulent. Roraima.

3a. LEDOTHAMNUS SESSILIFLORUS var. GLABER N. E. Brown l. c. Leaves glabrous except the ciliate margins. Roraima.

12. DABOECIA D. Don

The plant whose English name is Irish whorts, or, more poetically, Saint Dabeoc's heath, was known to Tournefort and to Ray, but was overlooked in the first edition of the *Species Plantarum*. It appeared in the second, but had already appeared earlier in the same year in Hudson's *Flora Anglica*, a work in which Linnaean usages are observed in detail. The two authors, Hudson and Linnaeus, pitched upon different genera of Octandria Monogynia for the accommodation of the plant, and on different key-words from the diagnoses of pre-Linnaean authors as specific epithets, producing respectively the combinations *Vaccinium cantabricum* and *Erica Daboecii*. In the case of this plant as of various others of the group, David Don was the first who validly published it in its proper generic position. The correct designation of the only species is to be ascribed to K. Koch, in spite of his attempt to correct the spelling of the generic name:

DABOECIA CANTABRICA K. Koch. *Vaccinium cantabricum* Hudson Fl. Angl. 143. 1762. *Erica Daboecii* L. Sp. Pl. ed. 2. 509. 1762. *Andromeda Daboecia* L. Syst. Nat. 2:300. 1767. *Erica Daboecia* L. f. Mant. 375. 1771. *Menziesia polifolia* Jussieu. *Daboecia polifolia* D. Don in Edinburgh New Phil. Jour. 17:160. 1834. *Daboecia cantabrica* K. Koch Dendrologie 2(1): 132. 1872. *Boretta cantabrica* O. Kuntze Rev. Gen. Pl. 2:387. 1891. Atlantic Europe: Azores, northern Portugal and Spain, southwestern France, western Ireland. Rehder (81) lists a number of cultivated varieties, differing in stature, size and color of flowers, etc.

For anatomical study, I have a specimen from a cultivated plant in the New York Botanical Garden.

The species is a shrub, of moderate size or low, with a pubescence of simple hairs and bristles many of which bear glands. No cylinder of fibers of pericycle was found in the vegetative stem; in the peduncle, on the other hand, this structure is well developed. The small pith has thick-walled tanniniferous cells at the margin and consists elsewhere of large, thin-walled, lightly staining cells.

The leaves are often opposite below and more than 1 cm. long (fig. 123),

alternate and smaller above, elliptic, revolute. They are about 130 μ thick (fig. 124). The upper epidermis is of large cells, the lower of smaller ones and beset with simple hairs. There are one or two layers of palisade cells, occupying about half of the thickness of the leaf. The veins are imbedded in the mesophyll. This description is in essential agreement with that of Breitfeld.

The flowers are borne in racemes terminal on the growth of the year (fig. 125), on pedicels perhaps 1 cm. long, in the axils of bracts to which there is a transition from the vegetative leaves, and without bractlets. They are tetramerous. The cylindrical urceolate corolla is usually pink and may exceed 1 cm. in length. Under the microscope, the cells of its external epidermis are columnar, projecting as papillae, densely tanniniferous.

The base of the receptacle is impressed, and the vascular system (fig. 126) may be described as resembling a cylinder which is greatly expanded for a short distance and pushed downward, forming a flat cone. Where the expansion is greatest, there emerges a whorl of eight large bundles. Four of these are main bundles of sepals, above which, separated from them by small gaps yet united to them by the margins, are the sepalad stamen bundles. The other four are petal bundles, each with two sepal laterals adnate below and a petalad stamen bundle adnate above. Higher on the cone, there arises a whorl of eight much smaller bundles, four of which are carpel dorsals and the other four carpel laterals which ascend the ovary wall in the planes of the septa and fade out at the summit of the ovary. The ovary being attenuate into the style, the carpel dorsals proceed smoothly into the latter without making a dip under a groove about its base.

The anther (figs. 127-135) has been described by Matthews and Knox. It is peculiar in being greatly elongate, sagittate-linear, with the filament attached near the base. The main bundle supplying the anther is directed to its base, but emits a branch running some distance toward the summit. Many of the epidermal cells on the outer surface and the inner margins project as papillae. The anther opens by the disappearance of bodies of resorption tissue which are broad in proportion to the slender summits of the lobes and attenuate below into slender columns descending no great distance.

Peltrisot published his account of the embryogeny in this genus as a preliminary to his survey of other members of the order (74). The ovules are rather few, about twenty in each locule; they show an exceptionally large number of layers of integumental cells between the jacket layer and the epidermis (fig. 137). The process of development from ovule to seed is essentially normal. The seeds are broadly ellipsoid, brown, warty, about 1 mm. long. They exhibit a number of peculiarities. All of the internal integumental cells are absorbed except the hypodermal layer; this layer, which is already recognizably differentiated in the ovule, survives intact, the cells being densely tanniniferous. The internal and lateral walls of the epidermal cells are extremely thick, even more so than in *Loiseleuria*, and traversed by even more attenuate channels; the thin outer cell walls are inflated, as Peltrisot says, like the fingers of a glove, and the lumina are densely tanniniferous (figs. 139, 140).

The numerous generic peculiarities of *Daboecia* suggest only the conclusion that this genus is particularly isolated, even among the Phyllodoceae.

Tribe IV. RHODOREAE D. Don

The tribe Rhodoreae as published by David Don was the same group as the present subfamily Rhododendroideae. It might have been expected, when the group was made a subfamily, that Don's name would be retained for the type tribe. Maximowicz, however, had already renamed the tribe Rhododendreae, because he recognized no genus *Rhodora,* and Drude followed him. Dalla Torre and Harms (20) treat Rhododendreae as the older name, ascribing it to Sprengel. Actually, Sprengel (100, 2:508) had neither published the name in Latin form nor as that of a tribe: his publication was of an *"Ordnung"* (included in *Familie Ericeen*) called *Rhododendreen.* Rhodoreae seems to have priority as a tribal name, and the objection that *Rhodora* is not maintained as a genus seems inconsequential.

The tribe is distinguished in the first place by the absence of resorption tissue in the anthers, which open through areas of collapse tissue. The disappearance of the collapse tissue leaves the pollen fully exposed, so that no contraction of the remainder of the anther wall is necessary. Except in the genus *Ledum,* fine filaments are present among the pollen tetrads. The haploid chromosome numbers, so far as they are known, are always 13 or 26.

The tribe is further characterized by winter buds protected by specialized scales. The flower-bearing axes bear, above these scales, no foliage leaves (*Therorhodion* affords, or appears to afford, an exception to this character). The bractlets, also, are characteristic: they are borne at the base of the pedicel, are linear, and are shed as the winter bud opens.

Eichler (26) was among the few authors who have maintained a family Rhodoraceae. He did this because of a feature of the floral diagram, namely (I change the manner of expression, but not the meaning) that the median petal is on the upper (ventral or adaxial) side of the flower. He noticed that *Azalea procumbens* (i. e. *Loiseleuria procumbens*) is an exception. To Hagerup (39) it seemed that this character is of little consequence. The fact appears to be that it distinguishes the tribe Rhodoreae (which is approximately the family Rhodoraceae of Klotzsch) from the other Rhododendroideae.

Finally, the Rhodoreae are generally large-leaved and often thin-leaved. Buxoid and erocoid leaves occur, but are not prevalent as among the Phyllodoceae.

In view of these characters, there is no doubt that the Rhodoreae are a natural group. It is presumed that the primitive anthers of the group are those of the genus *Tsusiphyllum,* which open by elongate slits broadened above. These anthers suggest the hypotheses, that the Rhodoreae are related most closely to the Cladothamneae, and that the lines of descent became distinct at an early stage, before the origin of the glabrescence and the peculiar embryogeny which characterize the Cladothamneae.

The anthers of *Menziesia* are transitional between those of *Tsusiophyllum*

and of the remaining genera. Among the latter, *Azalea*, obviously related as it is to *Menziesia*, is to be listed first. As among *Therorhodion*, *Azaleastrum*, *Rhododendron*, and *Hymenanthes*, the precise relationships are not evident; perhaps the order in which they are placed is inevitably subjective, all four being direct descendants of *Azalea*. *Ledum* is to be placed directly after *Rhododendron;* it is bound to this genus by common peculiarities of the pubescence, and its own peculiarities are evidently derived characters. The genera are distinguishable as follows:

1. Anthers opening by slits as long as themselves, broadened above.....13. *Tsusiophyllum*
1. Anthers opening by short slits broadened above.....14. *Menziesia*
1. Anthers opening by circular pores.
  2. Flowers sympetalous; fine filaments present among the pollen tetrads.
    3. Flowering axes without leaves or foliaceous bracts above the bud scales.
      4. Flowers terminal; leaves deciduous, or, if evergreen, beset with flattened bristles .....15. *Azalea*
      4. Not as above: if deciduous, then with lateral flowers; if evergreen, then without flattened bristles.
        5. Without glandular scales.
          6. Flowers lateral .....17. *Azaleastrum*
          6. Flowers terminal .....20. *Hymenanthes*
        5. With glandular scales .....18. *Rhododendron*
    3. Flowering axes with leaves (or rather, perhaps, foliaceous bracts) above the bud scales.....16. *Therorhodion*
  2. Choripetalous, without fine filaments among the pollen tetrads; with enlarged glands essentially resembling the glandular scales of *Rhododendron*.....19. *Ledum*

13. TSUSIOPHYLLUM Maximowicz

This genus includes a single species:

TSUSIOPHYLLUM TANAKAE Maximowicz in Mem. Acad. Sci. St. Pétersbourg sér. 7, vol. 16, no. 9: 12. 1870. Japan: Hakone Mountains. This is the most local of Rhododendroideae. Maximowicz saw a single collection, made by Tanaka and "Ycuttschima." I also have seen just one, in the Herbarium of the University of California.

The plant is a prostrate shrub with crowded alternate leaves 0.5-1 cm. long, broadly elliptic to obovate, cuneate, mucronate, entire, dark green and shining above, coriaceous. The stems bear simple and glandular hairs; both stems and leaves bear many rufous bristles. The terminal buds are globular, a few millimeters in diameter, covered by a few linear-spatulate scales with simple and glandular hairs and bristles on the back and margins. The scales are said to break up from the base; leafy branches in small numbers grow from their axils, with the effect that the branching appears di- or trichotomous. The higher scales subtend the few (1-3) flowers; the axis which bears them is so brief that they appear umbellate. Pedicels are about 2 mm. long. The five sepals are about 1 mm. long. The five petals are united in a cylindrical tube about 6 mm. long, white-hairy without and within, bearing spreading orbicular lobes about 2 mm. long. Maximowicz described the corolla as regular; to me it appears slightly irregular. Stamens five, anthers about 3 mm. long, extending to the

mouth of the corolla and opening by slits as long as themselves, wide near the apex and narrowed below. The carpels are described as three in number, but there is probably some variation. The pistil is as long as the corolla.

It is regretted that no material has been available for anatomical study, and that I have had to take the anatomical characters for granted. Perhaps some of them would turn out not to be characteristic of the tribe, but transitional toward it. While the anthers appear to be primitive, the leaves and the pattern of growth appear to be derived, and resemble those of *Azalea* subgenus *Tsutsutsi* (whence the generic name). The resemblance is presumably a matter of parallel evolution, not of direct relationship.

14. MENZIESIA Smith

The genus *Menziesia* commemorates Archibald Menzies, "the venerable," who collected *M. ferruginèa* in northwestern North America. Soon after it was described, Michaux transferred to it the closely related species of eastern North America. Subsequently, it was used as a dumping ground for rhododendroid and other plants whose true genera were undescribed or overlooked; *Bryanthus* and *Daboecia*, and all species of *Phyllodoce* except the latest, have been placed here. The brothers Don (22, 23) knew the true limits of the genus; it is evident that Klotzsch (53), whose Menziesiaceae are defined by a character contrary to that of the valid species, did not. Maximowicz, again, understood what *Menziesia* is. He described four new species from eastern Asia, and Nakai has added one more, making a total of seven:

I. Flowers pentamerous, calyx lobes elongate. Asiatic.
A. Flowers sordid, anthers elongate.
1. Stamens ten, flowers about 15 mm. long.

1. MENZIESIA CILIICALYX Maximowicz in Mem. Acad. Sci. St. Pétersbourg sér. 7, vol. 16, no. 9: 10. 1870. *Andromeda ? ciliicalyx* Miquel. Flowers umbellate, definitely zygomorphic, leaves elliptic. Japan.

2. MENZIESIA MULTIFLORA Maximowicz op. cit. p. 11. Flowers briefly racemose, nearly regular, leaves obovate. Japan.

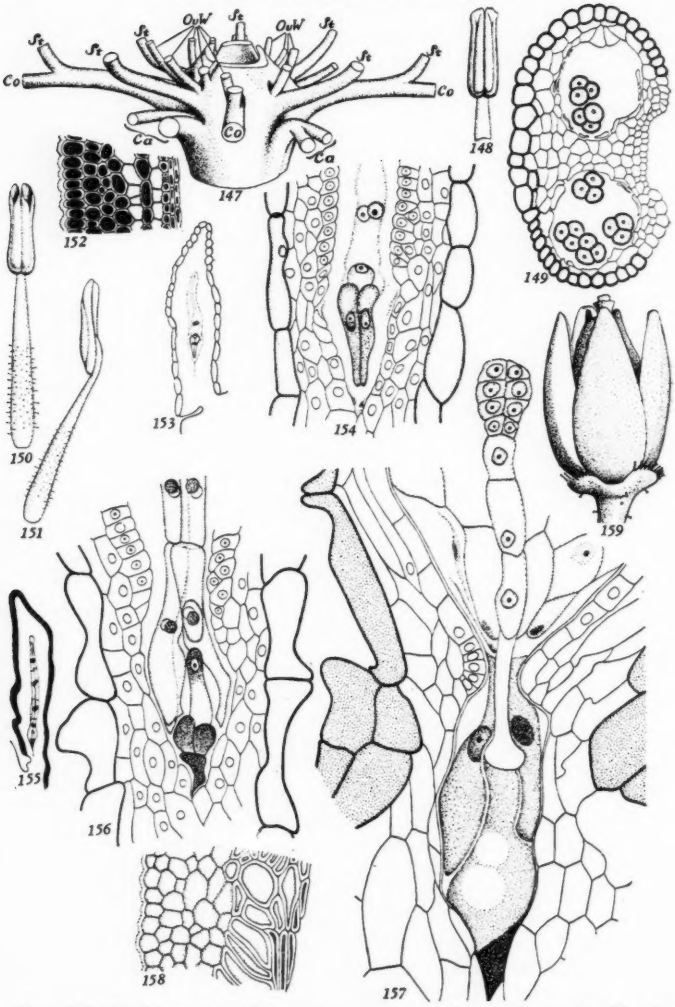
3. MENZIESIA LASIOPHYLLA Nakai. Very close to the preceding. Japan.
2. Stamens five, flowers about 8 mm. long.

4. MENZIESIA PENTANDRA Maximowicz in Bull. Acad. Sci. St. Pétersbourg 11:432. 1867. Sakhalin to Japan.
B. Flowers purple; anthers nearly as broad as long.

5. MENZIESIA PURPUREA Maximowicz l. c. Corolla about 15 mm. long, lobes dentate; filaments bristly. Japan: Kyushu.

II. Flowers tetramerous, calyx lobes short. Essentially American.

6. MENZIESIA FERRUGINEA Smith Pl. ined. t. 56. 1791. *Menziesia urceolaris* Salisbury Parad. Lond. under t. 44. 1806. *Menziesia globularis* Hooker Fl. Bor. Am. 2:41. 1834, non Salisbury. *Menziesia glabella* Gray Syn. Fl. 2(1):39. 1878. *Menziesia ferruginea* var. *glabella* Peck Higher plants of



Figs. 147-159. *Menziesia; M. ferruginea* except two figures representing *M. pilosa*. 147. Vascular system in floral receptacle ×40; labels as in fig. 29. 148. Young stamen of *M. pilosa* ×8. 149. Cross section of one lobe of young anther near summit ×160. 150, 151. Dehisced stamens ×8. 152. Portion of cross section of ovary wall ×160. 153. Longitudinal section of ovule ×64. 154. Micropylar portion of same ×320. 155. Longitudinal section of developing seed ×40. 156. Micropylar portion of same ×320. 157. Same, later stage, ×320. 158. Portion of cross section of wall of fruit ×160. 159. Dehisced capsule of *M. pilosa* ×4.

Oregon 542, Madroño 6:135. 1941. Seeds 2-3 mm. long. Typically the corolla is rather narrowly ellipsoid and at least 1 cm. long, the filaments pubescent; *M. glabella* represents plants with the corolla shorter and ovoid, the filaments glabrous. However, as Piper says (77, p. 440), "The characters relied on by Doctor Gray to distinguish his species break down completely." Kamchatka; Alaska to California and Idaho.

7. MENZIESIA PILOSA Persoon Syn. Pl. 1:420. 1805. *Azalea pilosa* Michaux. *Menziesia Smithi* Michaux Fl. Bor. Am. 1:235.1803. *Menziesia globularis* Salisbury Parad. Lond. t. 44. 1806. Seeds about 1 mm. long, corolla ovoid, to 7 mm. long, filaments pubescent; barely distinguishable from the preceding. Mountains, Pennsylvania to Georgia.

For anatomical study, I have material of *M. ferruginea* collected in coastal northern California and on Mount Rainier by Camp and by myself; of the same species collected near Juneau by the Juneau Botanical Club; and of *M. pilosa* collected on the Great Smoky Mountains in Tennessee by Camp. The two species appear identical in anatomical characters.

The plants are shrubs of the aspect of azaleas, as is indicated by Michaux's original assignment of *M. pilosa,* and by the American and Japanese common names mock azalea and *yoragu tsutsutsi.* Winter buds, young stems, leaves, pedicels, calyces, and ovaries are more or less densely beset with simple hairs (fig. 141), bristles, and glandular bristles (fig. 142). Anatomically, the young stems are in most respects typical of the subfamily (fig. 143 shows the typical wood, and the cork originating immediately within a cylinder of about three layers of fibers of pericycle); the pith consists entirely of small tanniniferous cells with thick pitted walls.

The leaves are crowded at the ends of the branches, petioled, fairly large, deciduous (notably thin), broadly elliptic or rhombic to obovate, apiculate. The epidermis is of large cells above, small ones below, with a thin cuticle on both sides. The palisade is for the most part of one layer of moderately elongate cells, occupying less than half of the thickness of the leaf (fig. 144). The veins are imbedded. These observations agree with Breitfeld's notice of this genus, which is to the effect that the anatomy of the leaves is as in *Azalea.*

Most terminal buds are swollen (fig. 145). Each such bud gives rise in spring to a corymb; there are no leaves or branches above the bud scales. Pedicels are from one to several centimeters long. In most species with pentamerous flowers, the corollas are definitely zygomorphic; in tetramerous flowers (fig. 146) the zygomorphy is barely perceptible.

I regret not having seen the vascular systems in the receptacles of the Japanese species, with their pentamerous flowers and well-developed sepals. In the American species there are irregularities indicative, I suppose, of reduction (fig. 147). Each sepal is supplied by one or two bundles arising at the base of a single gap. The petalad stamen bundles are adnate through a considerable distance to the petal bundles. The sepalad stamen bundles arise from the sides of the gaps above the sepal bundles. Fairly numerous ovary-wall bundles emerge immediately above the departure of the stamen bundles; the carpel

dorsals become distinguishable from the other ovary-wall bundles only some distance above their origin.

The slender anthers of the American species are attached near the base, and the vascular supply is by a single bundle running to the base, the upper two-thirds of the anther being without vascular tissue. In young anthers (fig. 148) the pollen sacs of each lobe are separated, near the summit, by sterile tissue. The triangular area of epidermis between their upper ends on the inner side of the lobe consists of collapse tissue, the cells being particularly small and thin-walled and the contents staining heavily with light green or aniline blue. This area is bordered by larger cells which stain similarly; all other epidermal cells stain heavily with saffranin, being tanniniferous (fig. 149). They are nowhere particularly columnar. At dehiscence, they are not contractile, but the light-staining cells bordering the areas of collapse tissue shrivel and form narrow inflexed borders around the pores.

The ovules (figs. 153, 154) is notably long and slender. The observed stages in the development of the seed (figs. 156, 157) conform to the description given as typical of the order. Peltrisot described the mature seeds as resembling those of *Rhododendron*, the internal integumental cells being absorbed at the sides of the endosperm but persisting as empty spaces at the ends of the seeds.

15. AZALEA L.

The Linnaean genus *Azalea* has been included in *Rhododendron* by the preponderance of authority during more than a hundred years. Correctly if somewhat awkwardly defined, as in the foregoing key to the genera of Rhodoreae, *Azalea* is clearly a natural group, having been so treated by Drude and by Rehder and Wilson (108). Its resurrection as a genus is expedient because of the inexpedient extent that *Rhododendron* has reached.

In the *Species Plantarum* (pp. 150-151) *Azalea* included six species:

1. *Azalea indica*. Wilson finds that this name covered two species. By Linnaeus' references to Breyn, Hermann, and Ray, he identifies as the true *A. indica* a plant commonly cultivated in Japan and formerly but no longer well known in the occident. The *Tsutsutsi* of Kaempfer is identified as a variety of *A. obtusa* Lindley. The two are closely related, representing the modern subgenus *Tsutsutsi*.

2. *Azalea pontica* is a plant of eastern Europe and Asia Minor which had been described by Tournefort under *Chamaerhododendros*, i. e., *Rhododendron*. Under *Rhododendron*, its name is *R. luteum* Sweet.

3. *Azalea lutea* is found to represent three American species. Among four publications cited by Linnaeus, that of Gronovius represents *A. canescens* Michaux; that of Colden represents *A. calendulacea* Michaux; those of Plukenet and of Linnaeus himself in the *Hortus Cliffortianus* are to be taken as typical. In the second edition of the *Species Plantarum* the name was changed to *A. nudiflora*, and the epithet there used, obviously invalid under *Azalea*, is valid under *Rhododendron*.

4. *Azalea viscosa* is an additional American species. The five species represented by *A. pontica, A. lutea,* and *A. viscosa* belong to the modern subgenus *Pentanthera.*

5. *Azalea lapponica* is a close ally of *Rhododendron ferrugineum,* misplaced because of its occasional pentandrous character.

6. *Azalea procumbens* is *Loiseleuria procumbens.*

Here, then, are representatives of four groups to which generic rank has been ascribed. Ascertainment of the type is important.

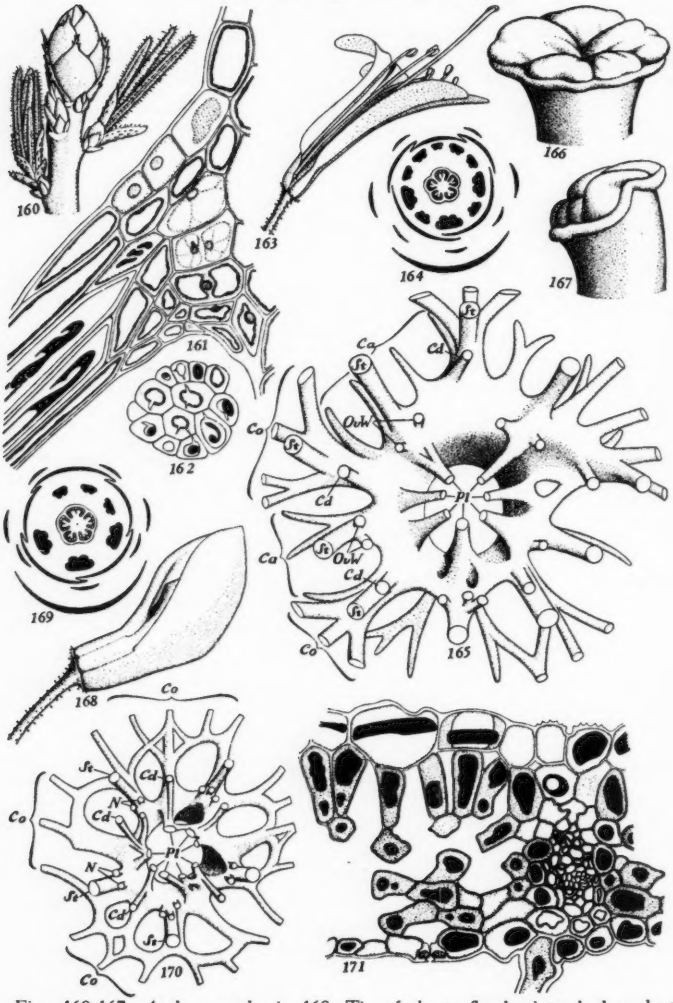
Small quite simply takes the first species, *A. indica,* as the type.

Whenever in the *Species Plantarum* Linnaeus used an older generic name and included more than one species, the previous history of the name should be considered in determining its application. Sometimes he deliberately reapplied a name: such, in the present group, are the cases of *Rhodora* and of *Ledum:* and in these cases we are bound by his action. More often, he changed limits, adding species, especially northern ones, to older genera. Inasmuch as his world-wide authority was based on knowledge of more than northern botany, he should in these cases be held to use the names in their older or original sense. According to these principles, and with much older authority, Rehder (82) holds that the type of *Azalea* is *A. procumbens.* The generic name was coined by Linnaeus himself in the first edition of the *Genera Plantarum* and appears to have been intended primarily to designate *A. procumbens* and *A. lapponica,* but the description fits only the former. If that is the true *Azalea,* the generic name of the group now under consideration would be, as Rehder points out, *Rhodora* L.

Kuntze (55) gives a different explanation of the origin of the name *Azalea.* He maintains that it was coined as a substitute for *Chamaerhododendros* Tournefort, that is, as a new name for what we call *Rhododendron;* this would mean that the original type was the species which we call *Rhododendron ferrugineum,* and that when, in 1753, Linnaeus founded *Rhododendron,* he deliberately shifted the application of *Azalea.* If this interpretation is tenable, *Azalea* was at the beginning of binomial nomenclature without a genuine type, and any type ascribed to it is an arbitrarily selected one, better called a standard species. The standard species should be so selected as to disturb subsequent nomenclature as little as possible; subordinate to this consideration, attention should of course be given to the relative antiquity of names. I conclude that *Azalea* is to be typified by *A. lutea,* to which Linnaeus had given a designation under this generic name in the *Hortus Cliffortianus,* in the same year, 1737, as the first edition of the *Genera Plantarum.*

It is not without conscious temerity that one fails to follow Rehder upon a point of nomenclature on which he has given judgment. Perhaps the foregoing discussion is mere rationalization for the purpose of allowing a large number of old names to stand.

Wilson and Rehder (108) treated the group as *Rhodendron* subgenus *Anthodendron* Reichenbach and divided it into four sections. In *The Species*



Figs. 160-167. *Azalea canadensis*. 160. Tip of shoot: floral winter bud ready to open, foliar winter buds opening, ×1.6. 161, 162. Longitudinal and cross sections of bristle of leaf ×320. 163. Flower ×1.6. 164. Floral diagram. 165. Vascular system in floral receptacle ×40; labels as in fig. 29. 166, 167. Stigmas ×20.

Figs. 168-170. *Azalea Vaseyi*. 168. Bud ×2. 169. Floral diagram. 170. Vascular system in floral receptacle ×20; labels as in fig. 29.

Fig. 171. *Azalea californica*. Cross section of leaf ×320.

of Rhododendron (98), Rehder treated the group as a series *Azalea* divided into six subseries. The following synopsis represents the earlier treatment, which may be consulted for synonymy beyond what is given here. Two of the subsidiary groups have been treated as subgenera of *Azalea*, while none bear names as sections under this genus; accordingly I place all of them in the category of subgenera, which is reasonable except possibly in the case of *Sciadorhodion*.

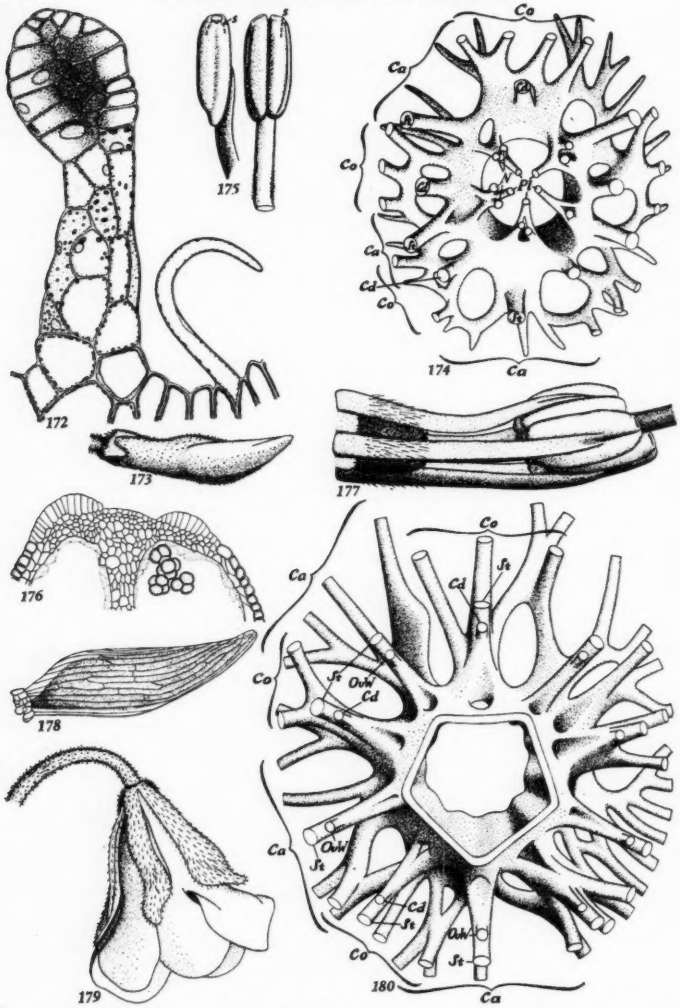
I. Terminal buds strictly floral, leafy shoots from lateral buds below. Flowers ordinarily numerous and evidently racemose. Leaves deciduous. Bristles present, not flattened.

A. Stamens ten, or at least more than five, except sometimes in *A. Vaseyi*; lobes of the corolla, at least in part, deeply separated, and the flowers wide open, except in *A. nipponica*.

Subgenus 1. **Rhodora** (L.) subgenus novum. *Rhodora* L. Sp. Pl. ed. 2. 561. 1762. *Hochenwartia* Crantz Inst. Rei Herb. 2:468. 1766. *Rhododendron* section *Rhodora* G. Don Gen. Syst. 3:848. 1834; Wilson and Rehder Monogr. Azalea 91, 119. 1921. This is surely the primitive subgenus. Leaves, pubescence, inflorescence and pattern of stamens are of types from which those found in the other subgenera can be assumed to be derived, being in fact the same as those of *Menziesia*. The evidence of the characters is supported by that of the number, distribution, and characters of the species: there are only five, three in Japan and two in eastern North America, almost every one markedly distinct: *A. canadensis* O. Kuntze (*Rhodora canadensis* L.; *Hochenwartia canadensis* Crantz; *Rhododendron Rhodora* Gmelin; *Rhododendron canadense* Torrey), North America, flowers red (rarely white), the two lower petals separate. *A. Albrechtii* (Maximowicz) O. Kuntze and **A. pentaphylla** (Maximowicz) comb. nov., Japan, flowers red, comparatively few, these species not as distinct from each other as the rest. *A. Vaseyi* Rehder (*Rhododendron Vaseyi* Gray; *Biltia Vaseyi* Small), from southeastern North America (mountains of North Carolina), sepals reduced almost to nothing, corolla red, blotched with yellow, upper petal outside the lateral ones in bud, stamens fewer than ten, sometimes only five. **A. nipponica** (Matsumura) comb. nov., Japan, flowers campanulate, white; Rehder (98, p. 73) places this in a subseries by itself.

B. Stamens strictly five. Corolla funnel-form with comparatively short lobes, the whole with more or less yellow color.

Subgenus 2. PENTANTHERA (G. Don) K. Koch Dendrologie 2(1):186. 1872. *Rhododendron* section *Pentanthera* G. Don Gen. Syst. 3:846. 1834; Wilson and Rehder Monogr. Azalea 95, 124. 1921. *Azalea* subgenus *Euazalea* K. Koch op. cit. p. 179. I do not use the subgeneric name which Koch placed first, because the second bears the older name and because the standard species *A. lutea* was assigned to the latter. *A. pontica* L. (*Rhododendron luteum* Sweet, type of the subgenus) in eastern Europe and Asia Minor. *A. mollis* Blume and *A. japonica* Gray in Japan. *A. lutea* L. (type or standard species of the genus; *A. nudiflora* L.; *Rhododendron nudiflorum* Torrey), *A. canescens* Michaux, *A. calendulacea* Michaux, *A. viscosa* L., **A. cumberlandense** (E. Lucy Braun under *Rhododendron*) comb. nov., and nine more species in eastern North America. *A. californica* Torrey and Gray (*Rhododendron occi-*



Figs. 172-177. *Azalea californica*. 172. Pubescence of pedicel ×320. 173. Bud ×2. 174. Vascular system in floral receptacle ×20; labels as in fig. 29. 175. Two views of stamen from a bud ×8. 176. Section of young anther in the plane marked *s* in fig. 175, ×80. 177. Stamens and pistil of a bud ×8.

Fig. 178. *Azalea subsessilis*. Seed ×40.

Figs. 179, 180. *Azaleastrum albiflorum*. VGT. Flower ×1.6. 180. Vascular system in floral receptacle ×40; labels as in fig. 29.

dentale Gray, *R. sonomense* Greene), California, most abundant on the northern coast, and coastal southern Oregon.

II. Leafy shoots from axils of the lower scales of the terminal bud. Flowers few, never yellow. Stamens from ten to five, often variable within the species.

A. Bristles absent from the stems, not abundant elsewhere. Leaves deciduous, crowded at the ends of the branches, generally large.

Subgenus 3. **Sciadorhodion** (Rehder and Wilson) subgenus novum. *Rhododendron* section *Sciadorhodion* Wilson and Rehder Monogr. Azalea 79. 1921. Intermediate between the subgenera *Rhodora* and *Tsutsutsi*. *A. Schlippenbachii* (Maximowicz) O. Kuntze, **A. Mariesii** (Hemsley and Wilson under *Rhododendron*) comb. nov., and four other species from Japan and eastern China.

B. Plants beset with flattened bristles; leaves at least in part evergreen.

Subgenus 4. TSUTSUTSI (G. Don) K. Koch Dendrologie 2(1):171. 1872. *Tsutsutsi* of Kaempfer and Adanson, apparently never published in combination. *Rhododendron* section *Tsutsutsi* G. Don Gen. Syst. 3:845. 1834; Wilson and Rehder Monogr. Azalea 22. 1921. In **A. Tashiroi** (Maximowicz) comb. nov., from southern Japan, the leaves resemble those of subgenus *Sciadorhodion*, and Rehder (98, p. 121) places it in a separate subseries. In the remaining species the leaves are of two kinds, large, thin, deciduous spring leaves and smaller thicker summer leaves, the latter, or the highest among them, evergreen. *A. indica* L. (type of the subgenus; according to Small, type of the genus), *A. obtusa* Lindley, and *A. rosmarinifolia* Burmann (*Rhododendron mucronatum* and *R. ledifolium* G. Don), from Japan; **A. Simsii** (Planchon) comb. nov. from China, confused with *A. indica* in gardens; seventeen more species from the same countries together with Korea and Formosa; **A. subsessilis** (Rendle) comb. nov. in northern Luzon.

For anatomical study I have representatives of subgenus *Pentanthera* collected by Camp in the eastern United States, but have concerned myself chiefly with *A. canadensis* and *A. Vaseyi* furnished by the Arnold Arboretum, and with specimens of *A. californica* collected by Mrs. Dorothy Siler and by myself in coastal northern California.

The plants are shrubs, sometimes fairly large, sometimes prostrate. The presence of bristles (figs. 161, 162) has been noted in the synopsis above. There are also simple hairs and glandular bristles (figs. 171, 172). The anatomy of the stem is that which is normal to the Rhododendroideae, the pericycle consisting of two or three layers of fibers.

I have studied the microscopic structure of the leaves only in *A. californica* (fig. 171). In this species, being deciduous, they are thin (about 125 μ thick) and have a thin cuticle. The cells of the upper epidermis are decidedly larger than those of the lower. The palisade is a single layer of moderately elongate cells and occupies less than half of the thickness of the leaf. The veins are imbedded. These observations agree with Breitfeld's in all points except one: he construes the veins as "*durchgehend*", i. e., as attached through flanges of fibers to the epidermis. I do not feel that his observations were mistaken, but that we have placed different interpretations on a borderline case. As to the

leaves of subgenus *Tsutsutsi,* which I have not seen, he furnishes the information that they are of essentially the same structure but of somewhat greater thickness.

Extensive description of winter buds, inflorescences, flowers, and most flower parts would be repetitious; the pattern of stamens alone requires discussion. The normal number of stamens is ten. They are doubly differentiated: those of the sepalad whorl are larger than those of the petalad whorl, and in each whorl there is an increase in size from the upper (ventral, adaxial) side of the flower to the lower (dorsal, abaxial) side. Thus the uppermost stamen is the smallest, and on the lower side there are three large ones of the sepalad whorl alternating with two smaller ones of the petalad whorl. The pattern described is exhibited in full by *A. canadensis* (fig. 164) and by some species of subgenus *Tsutsutsi.* In *A. Vaseyi* (fig. 169) and in various species of subgenus *Tsutsutsi,* some of the petalad stamens are lost: the one opposite the highest petal goes first, then the ones opposite the lower petals, finally the ones opposite the lateral petals; the number remaining may vary freely from five to ten on a single plant. In some species of *Tsutsutsi* and throughout *Pentanthera* (fig. 177) the petalad whorl is constantly absent.

The vascular system in the floral receptacle is not uniform. That of *A. canadensis* (fig. 165) may be described first. The receptacle is broad but not impressed from below. Within it the siphonostele ascending from below flares broadly. A number — say from two to five — of rather feebly developed bundles run out to each sepal. These may emerge from the margins of the flared siphonostele, or from below the margin, leaving small gaps; or from the sides of the petal bundles; and they may to some extent anastomose with the petal bundles and with each other. The petals are supplied by large and well-marked bundles which, except as they may be enlarged by branches from the sepal bundles, emerge from the margins of the flare; in general, the supply to each petal originates as a single bundle, but there may be two or more. Petalad stamen bundles are adnate through some distance to the petal bundles, or, where these are more than one, to the main petal bundles. Sepalad stamen bundles are large and definite bundles emerging from the margin of the flare alternately with the main petal bundles. Carpel dorsals, and slender additional bundles supplying the nectary and ovary wall, ascend instead of spreading from the margin of the flare; the carpel dorsals may be briefly adnate to the combined petal and petalad stamen bundles. The flared siphonosteles of genera described before this, as for example of *Daboecia,* have been described as contracting above the flare to supply the central column of the ovary and the placentae. In the present case, the stele will better be visualized as breaking up at the margin of the flare; the central column and placentae are supplied by a whorl of small bundles originating inside the stele below the margin and running upward and inward.

In *A. californica* (fig. 174) one sees in the receptacle the same broadly flaring stele breaking up at the margin into separate bundles. One may make out, in the prevalent irregularity, a tendency for these to be ten in number, the five in the planes of the sepals emerging at a slightly lower level. These

bundles do not directly supply the perianth parts; they fork and anastomose, forming loops; from the loops arise further bundles in considerable number, perceptibly in two tiers; those of the lower tier supply the sepals, and those of the upper the petals. The stamen bundles come off the edges of the flare above the main perianth bundles which are in the planes of the sepals, and the carpel dorsals arise similarly in the planes of the petals. The supply to the central column of the ovary and the placentae originates as five rather small bundles, on the inside of the stele, not far from the margin, and in the planes of the sepals. The insignificant nectary bundles and ovary wall bundles in addition to the carpel dorsals arise from the bases of the placental bundles.

The diagram of the vascular supply in the receptacle of *A. Vaseyi* (fig. 170) was constructed from sections of a flower with only five stamens. It is quite like that of *A. californica* with one noteworthy difference. As in *californica,* the ten main perianth bundles fork and anastomose with each other, forming loops. All the bundles from these loops run to the corolla; the reduced sepals are without vascular supply.

The epidermis of the anthers is for the most part tanniniferous, yellowish in fresh material. On young anthers (fig. 175), above the upper end of the groove on each lobe and overlying the ends of both pollen sacs, there is a depressed small area, nearly circular but slightly pointed below, white in color; this is surrounded by an elevated white border. Microscopic examination shows that the elevated border is of somewhat columnar cells without tannin, and that the depressed area is of small cells which stain heavily with aniline blue or light green (fig. 176). This is an area of collapse tissue; the internal cells, beyond the hypodermal layer, and excepting of course the pollen tetrads, are likewise of collapse tissue; dehiscence is accomplished by their disappearance, which leaves a circular hole, surrounded by a definite border, in the epidermis of the anther. The description just given is exactly that of *Rhododendron* (understood, of course, to include *Azalea*) by Artopoeus and Matthews and Knox.

The ovules are elongate. Developing and ripe seeds in preservative have not come to hand; the essential agreement of *Azalea* with *Menziesia* on the one hand, and with *Ledum* and *Hymenanthes* on the other, gives assurance that there are no marked peculiarities here. Peltrisot saw ripe seeds of *A. japonica* and *A. mollis.* These are strongly flattened between placenta and pericarp. A plane parallel to the broad faces of the seed separates the cotyledons, which are likewise broad and flat. The empty cell walls of internal integumental cells persist in the ends of the seed, and imbedded among them are the remains of chalazal and micropylar haustoria. At the chalazal end, the integument forms a smooth wing; at the microplyar end, the wing is distorted by irregular outgrowths, almost plumose. In subgenus *Tsutsutsi* (*A. subsessilis,* fig. 178), the seeds are not flattened and the wings are reduced.

16. THERORHODION (Maximowicz) Small

Rhododendron camtschaticum Pallas was described as occurring on the Okhotsk Coast and in Kamchatka (in the text of the original description, the

epithet is spelled as here, but on the accompanying plate it is spelled with a *k*. I use the *c* as presumably representing the intention of the author, being better Latin). It has subsequently been discovered in western Alaska, and two allied species have been discovered in the same general area. These plants have never been generally familiar. Whenever studied, they have seemed more or less anomalous in *Rhododendron*. Lindley placed *R. camtschaticum* in *Rhodothamnus;* Maximowicz set up a distinct section of *Rhododendron* for it; Small raised this to generic rank.

The plants are low or prostrate shrubs with simple hairs, bristles, and glandular bristles. The leaves are elliptic or obovate, apiculate, nearly glabrous except the ciliate margins, thin but firm, the veins prominent especially on the lower surface. It seems (the authorities are not definite on this point) that they are not long-lived, but that some of them may survive the winter. The flowers are borne on long pedicels, terminal or in the highest axils of what appear to be the leaf-bearing shoots of the year. Wilson (107) criticizes this accepted interpretation of the inflorescence. He interprets it as essentially the same as the leafless corymb usual in Rhodoreae, specialized in that the flowers are few and the axis elongate, and that the bracts simulate foliage leaves. The sepals are separate, spreading; the rose-purple corolla is broadly open, the sinuses deep, the one between the two lower petals extending to the base of the corolla. The stamens are ten, the filaments pubescent below, with a sort of angle or hump at the summit. They are said to be unequal in length and declined; presumably the pattern is the same as the one described as typical for *Azalea*. The pistil is of five carpels; the ovary pubescent, narrowed in the upper part, impressed at summit; style elongate, pubescent below; stigma capitate. The capsule is thin-walled, opening by brief slits between the carpels at the summit.

The species are distinguishable as follows (cf. Tagg, 98, p. 187):

I. Corolla exceeding 4 cm. in diameter, the lobes exceeding the tube.

A. Corolla externally pubescent.

1. THERORHODION CAMTSCHATICUM Small in North Amer. Flora 29:45. 1914. *Rhododendron camtschaticum* Pallas Fl. Ross. 1:48. 1784. *Rhodothamnus camtschaticus* Lindley. Okhotsk Coast, northern Japan, Kamtschatka, western Alaska.

B. Corolla externally glabrous.

2. THERORHODION GLANDULOSUM Standley ex Small in North Amer. Flora 29:45. 1914. *Rhododendron glandulosum* Tagg in Sp. Rhodod. 190. 1930. Known, apparently, only by the type collection "at the foot of Kigluaik Mountains, near Oogluk Bay, Imuruk Basin, in the vicinity of Port Clarence, Alaska."

II. Corolla smaller, the lobes equalling or shorter than the tube.

3. THERORHODION REDOWSKIANUM Hutchinson. *Rhodothamnus Chamaecistus* Ledebour non Reichenbach. *Rhododendron Redowskianum* Maximowicz Prim. Fl. Amur. 189. 1859. Eastern Siberia; type locality "prope Jablonnoi Chrebet vel ipsas alpes inhabitans."

Of this genus I have seen nothing except a few herbarium specimens of *T. camtschaticum*. Breitfeld gives a figure of the cross section of the leaf, with all characters as in *Azalea*. Peltrisot saw the seeds, which are essentially as in *Azalea* and *Rhododendron*.

17. AZALEASTRUM (Planchon) Rydberg

Planchon referred *Rohdodendron ovatum* and *R. albiflorum* to a new subsection *Azaleastrum;* Maximowicz raised this to sectional rank, and added *R. semibarbartum;* Rydberg made it a genus, publishing a combination, naturally, only for the single species which occur in his area. The type species of the genus, therefore, is *Azaleastrum albiflorum* Rydberg in Mem. New York Bot. Gard. 1:297. 1900 (*Rhododendron albiflorum* Hooker Fl. Bor. Am. 2:43. 1843. *Cladothamnus campanulatus* Greene in Erythea 3:65. 1895).

The plants are of all sizes up to arboreal. The group is distinguished only by the inflorescence, taken in connection with the absence of scales. From terminal buds arise the leafy continuations of the stem: flowers emerge from subterminal axillary buds and may be umbellate (i. e., in a condensed raceme), several or few, or solitary.

The classification is as follows. Having no personal knowledge of most of the species, I refrain from making new combinations.

I. Leaves deciduous, sepals prominent.

A. Stamens ten (to twelve).

Series 1. ALBIFLORUM. The single species *A. albiflorum,* in the northern Rocky Mountains of North America as far south as Montana and Oregon.

B. Stamens five, the two upper greatly reduced.

Series 2. SEMIBARBATUM. A single species in central and southern Japan.

II. Leaves evergreen.

A. Stamens ten, sepals prominent.

Series 3. STAMINEUM (the group *Choniastrum* Franchet, construed by Drude as a subgenus of *Rhododendron*). Sixteen species: Burma, southern China and Hongkong, Formosa; one in the Malay Peninsula, none on the Malay Islands.

B. Stamens five, sepals obsolescent.

Series 4. OVATUM. Five species, northeastern, southern and western China to eastern Tibet.

For anatomical study I have flowers only (fig. 179) of *Azaleastrum albiflorum* collected by Camp on Mount Rainier. Many of the flowers are peculiar in being hexamerous. Pedicels, sepals and ovaries bear many simple hairs and glandular bristles.

The vascular system in the floral receptacle (fig. 180) is in the form of a cylinder which expands as it ascends from below and contracts above to supply the central column of the ovary and the placentae. At the level of greatest expansion there emerge more than ten bundles, but not many more; these are indefinitely in two whorls, the lower opposite the sepals, the higher opposite the petals. Above most of them there are gaps. They fork and anasto-

mose with a certain freedom, forming loops, and giving rise to a large number of bundles which are now definitely in two tiers, supplying respectively the sepals and the petals. Petalad stamen bundles and carpel dorsals arise from the upper sides of the main perianth bundles which are in the planes of the petals. Sepalad stamen bundles arise separately from the perianth bundles, above the gaps above the main perianth bundles in the planes of the sepals. Each of these, before it enters the stamen it is to supply, sends out from the adaxial side a branch which ascends the ovary wall in the plane of a septum; one may say that the fused carpel laterals of adjacent carpels are adnate to each sepalad stamen bundle.

Stamens have been seen only after dehiscence. They are altogether as in *Azalea*. All features of the elongate ovule (fig. 181) ar already familiar.

18. RHODODENDRON L.

The name *Rhododendron* originated in the *Species Plantarum* (p. 392). It is a substitute for the *Chamaerhododendros* of Tournefort; the second such substitute, as Kuntze tells us, *Azalea* having been the first. As originally published it included five species:

1. *Rhododendron ferrugineum*, a small shrub of the Alps, with scaly herbage and tubular-funnelform red flowers. It is the most familiar among a small number of plants to which the common name *Alpenrose* is commonly applied. Compelled as we are to recognize types in pre-type-system publication, we are surely correct in recognizing this as the type of *Chamaerhododendros* and of *Rhododendron*.

2. *Rhododendron dauricum* is said to have glabrous leaves and to inhabit "Dauria." The plant to which this name is known to apply actually has the leaves scaly beneath, and occurs from central Asia eastward to Japan. It exhibits details of inflorescence distinguishing it from the other original species of *Rhododendron*.

3. *Rhododendron hirsutum* is a close ally of *R. ferrugineum*, and comes from the same region. As noted above, the *Azalea lapponica* published with these species is another reasonably close ally.

4. *Rhododendron Chamaecistus* is *Rhodothamnus Chamaecistus* Reichenbach.

5. *Rhododendron maximum* is a large shrub or small tree of eastern North America, with large leaves totally without scales. Its closest ally in the Old World is *R. ponticum* L. Sp. Pl. ed. 2. 562. 1762, from Asia Minor.

According to Wilson (108, p. 16), "Salisbury (*Prodr.* 286 (1796)) was the first to point out that Azalea and Rhododendron could not be maintained as distinct genera," and G. Don (23) was the first to carry through the reduction, making new combinations for all species previously known as *Azalea*. If one exclude the type species of *Loiseleuria* and *Rhodothamnus*, the rest of the Linnaean species of *Azalea* and *Rhododendron* constitute indisputably a natural group; as soon as the sexual classification of Linnaeus was abandoned, the two genera seemed to melt into one convenient genus as set forth by G.

Don and by Endlicher. Europe, North America, and western Asia, taken together, harbor but a moderate number of species; Africa and South America have none. It was explorations in northwestern India and beyond, especially those of the younger Hooker (44), that first showed that there are more species in the group than had been suspected. Comparatively recent explorations in the near-by regions (as they appear on a small-scale map) of western China and Tibet have yielded actual hundreds of species. The Malay Archipelago, including New Guinea, has been shown to be a center of distribution second only to this. It is undesirable that a genus as extensive as the accepted genus *Rhododendron* be maintained; and it is unnecessary to maintain it if a system of smaller groups which are both natural and definable can be set up.

Three contributions bearing on the natural subdivision of the accepted genus *Rhododendron* are particularly to be noted.

The first of the three is that of Maximowicz, who subdivided primarily on the basis of the inflorescence. The treatments of the genus by Bentham and Hooker and by Drude are based on this.

The latest of the three is to be found in *The Species of Rhododendron* (98). Here the attempt at a primary classification is abandoned; no subgenera nor sections are set forth; instead of these, forty-three series, based on the work of the late Sir Isaac Bayley Balfour, are presented in the alphabetic order of their typical species. It was found necessary, in this work, to overlook the species of the Malay Region. Beside noting these acknowledged deficiencies, one observes that a considerable number of new species are described in English; that one of the authors fails to cite the publication of the species with which he deals; and that another fails to designate type specimens of new species. It remains true that this is a supremely useful work, recognized as such by all who are concerned with the group. To one who is concerned primarily with classification, it is useful as a thorough piece of analysis, the overwhelming mass of species being arranged in groups small enough to be reasonably uniform and not too numerous for comparison.

Intermediate in time of publication between the work of Maximowicz and *The Species of Rhododendron* was the contribution of Rehder (81). Setting apart *Azalea*, *Therorhodion*, and *Azaleastrum*, he arranged the remaining species in two groups on the basis of a detail of pubescence: those which bear scales make up the section *Lepidorhodium;* those which do not are *Leiorhodium*. This arrangement is not recognized in the text of *The Species of Rhododendron*, but the introduction points out that the assignment of series for treatment, respectively by Tagg and by Hutchinson, was guided by it. I believe that it represents the desired subdivision of the currently accepted genus *Rhododendron* into smaller groups which may be accepted as genera; and that the generic name is to be restricted to a group coinciding with Rehder's section *Lepidorhodium*.

The following is an attempt at subgeneric organization.

Subgenus 1. RHODORASTRUM C. B. Clarke in Hooker f. Fl. British India 3:474. 1882. Section *Rhodorastrum* Maximowicz in Mem. Acad. Sci. St.

Pétersbourg sér. 7, vol. 16, no. 9: 15. 1870. Maximowicz founded this group to include *R. dauricum* L. and *R. mucronulatum* Turczaninow, shrubs which are more or less deciduous, with flowers in small numbers from lateral buds, the corollas wide open and deeply cut. The characters suggest the possibility that these species are transitional between *Azalea* and *Rhododendron* proper. I propose to use this group as a catch-all for all species not falling into the better-marked subgenera considered below. Here are all that have large leaves and large wide-open flowers; all with a tendency to have pistils with more than five carpels (this is a derived character, but one that appears repeatedly and at a low level of evolution); several that are notably bristly; just one, *R. Augustinii,* with a pubescent ovary. These make up, in *The Species of Rhododendron,* the series *Camelliaeflorum, Dauricum, Edgeworthii, Glaucum, Maddenii, Moupinense, Saluinense, Scabrifolium, Trichocladum, Triflorum,* and *Virgatum,* with a total of 148 species. *R. dauricum* and *R. mucronulatum* occur in northeastern Asia, *R. Keiskei* in Japan. Whether any of the Indo-Chinese species may belong here I do not know. Certain Bornean species suggest *R. Edgeworthii.* For the rest, the group is confined to the Himalayas, Tibet, northern Burma, Szechwan, and Yunnan. It is believed that this miscellany includes the primitive forms of the genus *Rhododendron* as here limited, being the ancestors of the following subgenera. Presumably future study will reveal additional groups to be segregated from the present unsatisfactory one.

Subgenus 2. VIREYA C. B. Clarke in Hooker f. Fl. British India 3:462. 1882. *Vireya* Blume Bijd. 854. 1826. Terrestrial, to the size of small trees, or epiphytic; leaves and flowers generally large; floral buds terminal and strictly floral; bud scales not ciliate; corolla usually funnelform; ovary pubescent, glabrous, or sparsely lepidote, not densely lepidote; fruits elongate, the string-like placentae becoming detached in dehiscence; seeds long-tailed. Type, *R. javanicum* (Blume) Bennett. Among more than two hundred species in the areas not considered in *The Species of Rhododendron,* the great majority belong here: one may estimate the number as 175, essentially confined to the Malay Peninsula and Archipelago (including New Guinea). *R. Lochae* von Mueller in Queensland; possibly some representatives in Indo-China. Schlechter (90) and I (17) have undertaken the subordinate classification of the representatives within limited areas into groups which should be given the rank of sections. I am afraid that when a comprehensive organization in sections is undertaken these essays will be found to have created more confusion than enlightenment.

Subgenus 3. EURHODODENDRON Endlicher Gen. Pl. 759. 1840 (?). Sections *Ponticum* and *Lepipherum* G. Don Gen. Syst. 3:843, 845. 1834, in part; section *Osmothamnus* Maximowicz in Mem. Acad. Sci. St. Pétersbourg sér. 7, vol. 16, no. 9: 14. 1870, in part; series *Graveolentes* Bentham and Hooker Gen. Pl. 2:600. 1876; section *Lepidorhodium* Rehder in Bailey Std. Cycl. Hort. 5:2937. 1916, for the most part. Shrubs or trees, some Malayan species epiphytic. Leaves prevalently small, elliptic to oblanceolate, apiculate to retuse. Floral buds terminal and strictly floral. Bud scales ciliate. Corolla funnelform; the lobes may be spreading but are then comparatively small. Ovary densely

lepidote. Series to be included here are *Campylogynum, Carolinianum, Ferrugineum, Heliolepis, Lapponicum, Micranthum,* and *Vaccinioides,* a total of sixty-two species, widespread in the area of *The Species of Rhododendron,* but particularly abundant in the Himalaya-Yunnan area. Hutchinson was correct in pointing out that the series *Vaccinioides* includes Malayan representatives; among these are *R. Quadrasianum* and *R. retusum.* He was in my opinion mistaken in maintaining *R. rosmarinifolium* as a species distinct from *R. Quadrasianum,* and in placing *R. Vidalii* in this group; it is a *Vireya.* Another insular group belonging here may be designated the series *Malayanum: R. malayanum, R. apoanum, R. Nortoniae, R. catanduanense,* and others in the islands to and including New Guinea. These may raise the total membership of the subgenus to one hundred species.

Subgenus 4. **Pogonanthum** subgenus novum. Section *Pogonanthum* G. Don Gen. Syst. 3:845. 1834; section *Lepipherum* G. Don l. c. in part; *Osmothamnus* DC. Prodr. 7(2):715. 1839; series *Osmothamnus* Bentham and Hooker Gen. Pl. 2:601. 1876. Shrubs much as in *Eurhododendron;* corolla salverform. The group was founded by Don for *R. anthopogon* only; this species represents an extreme development, the corolla strongly pubescent within, stamens usually fewer than ten. Don's section *Lepipherum* was a miscellany; *R. lepidotum,* which is presumably the type, being the first species listed, is a reasonably close ally of *R. anthopogon.* De Candolle's genus *Osmothamnus* is the same group as series *Cephalanthum,* which also belongs here; as a subgeneric group, of Maximowicz and even more of Breitfeld, it tended to include the whole genus *Rhododendron* as here construed. The subgenus here established is to include, of course, the series *Anthopogon, Cephalanthum,* and *Lepidotum* of *The Species of Rhododendron,* with a total of thirty-five species confined to the Himalaya-Yunnan area.

Subgenus 5. KEYSIA Nuttall ex Hooker in Bot. Mag. t. 4875. 1855. Shrubs, flowers numerous from axillary buds, corolla cylindrical with erect lobes. *R. Keysii* and *R. cinnabarinum.* Sikkim, Bhutan.

The estimated number of known species of *Rhododendron,* then, is 460.

The present studies had reached an advanced stage before I realized that in studying *Rhododendron californicum* and *Azalea californica* I was not studying *Rhododendron* in the strict sense at all. My belated efforts to secure material of *Rhododendron* proper brought me just one species, *R. micranthum* Turczaninow, for which I am indebted to the University of California Botanical Garden. This shrub from northern China, with small white flowers in extended racemes and glabrous filaments, is assigned to a series by itself; I believe nevertheless that it is perfectly at home in, and a satisfactory representative of, the type subgenus *Eurhododendron.*

More or less numerous simple hairs are found in *R. micranthum* on the epidermis of stems, bud scales, pedicels, sepals, and ovaries. The bud scales throughout subgenus *Eurhododendron* are ciliate with these, and the filaments of most species are pubescent with them. Bristles were noted on *R. micranthum* only as a ciliate margin to the sepals, and I find none of those glandular bristles which are so conspicuous in most genera of Rhododendroideae.

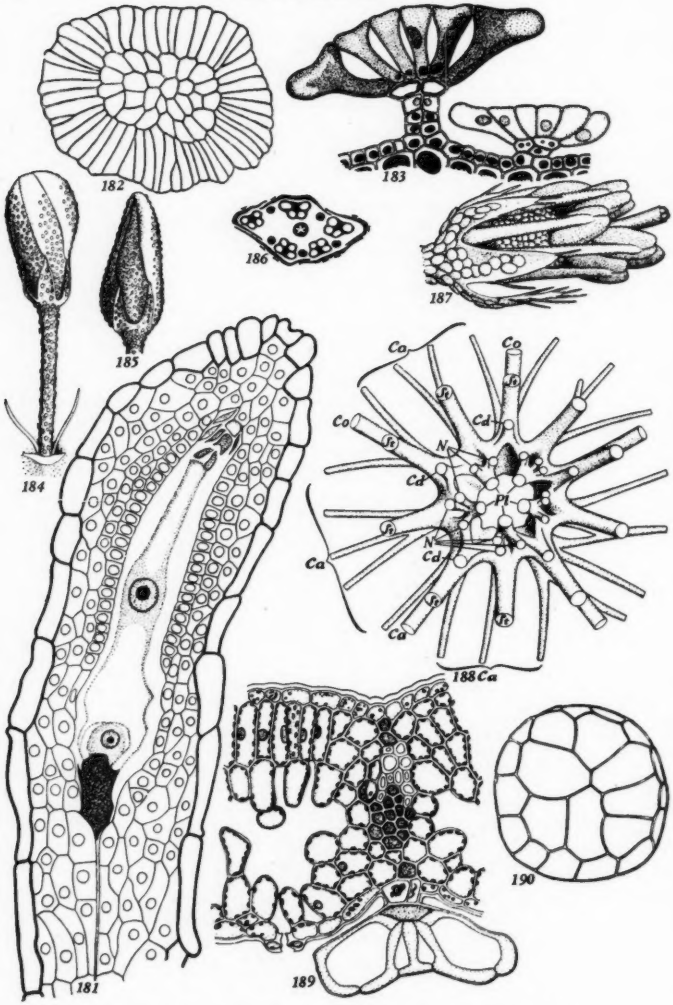


Fig. 181. *Azaleastrum albiflorum*. Longitudinal section of ovule ×320.

Figs. 182-188. *Rhododendron micranthum*. 182. Scale of the lower surface of the leaf ×160. 183. Sections of scales of ovary ×320. 184, 185. Buds ×4. 186. Cross section of bud ×8. 187. Bud with corolla removed ×8. 188. Vascular system in floral receptacle ×40; labels as in fig. 29.

Figs. 189, 190. *Ledum glandulosum*. 189. Cross section of leaf ×320. 190. Gland of leaf, surface view, ×320.

More conspicuous than the types of pubescence just discussed is that which consists of "scales" or "lepides," occurring on the parts already mentioned and also on the leaves; in *R. micranthum*, as in many other species, sparsely above and densely below. Each of these (figs. 182, 183) consists of a stalk and a cap. The stalk is usually of two series of cells and is rather short, often only one cell long. The cap is a single tier of cells in the form of cones attached to the stalk by the small end and laterally in contact with each other. Those at the margin of the tier are radially extended. All of these cells are glandular; as they mature, they shrink in the middle, becoming tack-shaped and losing mutual contact except at the extremities.

It is by scales of precisely this character that the genus *Rhododendron* is here limited. Their essential difference from those of *Rhodothamnus Leachianus* is, I think, obvious. They have been illustrated as occurring in various species by Vesque (105), Breitfeld, and Hegi (41), and I have seen them, in preparations made from herbarium material of *R. apoanum, R. Kochii,* and *R. taxifolium,* so precisely as in *R. micranthum* as not to require illustration. Breitfeld has listed *R. caucasicum* as a typical example: most authors list this species as elepidote, and I do not understand its appearance in this connection. He described, in *R. pendulum, R. hirsutum, R. Dalhousiae,* and *R. anthopogon,* variant forms which seem to connect these scales with the glands, for example, of *Azalea.* I am sure that this represents the actual phylogenetic derivation, but I do not recognize *R. hirsutum* and *R. anthopogon* as occupying an intermediate position in the evolution of the genus.

In microscopic structure, the stems of *R. micranthum* conform to that which is typical of the Rhododendroideae, except that the pericycle is reduced to an incomplete single layer of fibers.

The leaves of *R. micranthum* are about 300 μ thick. The epidermis is on both sides of small cells with a heavy cuticle. There are about three layers of moderately elongate palisade cells, occupying slightly less than half of the thickness of the leaf. The veins show only traces of fibrous flanges above and below. Breitfeld has reported agreement in the structure of the leaves between (1) *R. anthopogon;* (2) several species of the series *Graveolentes* of Bentham and Hooker, which, accordingly, he reduced to *Osmothamnus;* and (3) *R. punctatum,* a species of series *Carolinianum,* which, following Bentham and Hooker, he took for a *"Eurhododendron."* All these agree well with *R. micranthum* as just described, except that they have well developed flanges of fibers connecting the veins with the epidermis above and below. I take these observations as strong evidence for Rehder's view, on which I base the limits here given to the genus *Rhododendron,* that all the lepidote species constitute a natural group.

It must be said that Breitfeld found a sharply distinct type of structure in the Malayan species (the subgenus *Vireya* together with certain species here construed as belonging to *Eurhododendron*). They have a layer of large thin-walled water-storing cells under the upper epidermis, and the veins are concen-

tric, imbedded between palisade tissue and spongy tissue, and surrounded by thin-walled transfusion cells.*

The floral buds of *Rhododendron* are strictly floral, and are terminal except in *Keysia* and a few species of *Rhodorastrum*. The flowers are essentially as in *Azalea*, with the same weak zygomorphy and the same pattern of stamens (figs. 186, 187) with the same variations. The corollas are generally narrower, with narrower sinuses.

In the floral receptacle of *R. macranthum* (fig. 188) there is a distinct whorl of about ten sepal bundles. These fork and anastomose to some extent, and their number may be increased by occasional branched descending from the petal bundles. The outcome is the supply of each sepal by about three bundles. There is a definite whorl of five petal bundles, to which the petalad stamen bundles are briefly adnate. The sepalad stamen bundles arise independently at about the same level. Above the stamen bundles there are gaps in the comparatively scant cylinder of vascular tissue which ascends beyond them. This breaks up into five carpel dorsals and five bundles which swing inward to supply the central column of the ovary and the placentae. From the bases of the latter spring a certain number of ovary-wall bundles in addition to the carpel dorsals.

I have no undehisced anthers. After dehiscence, they are exactly as in *Azalea*, and there is no doubt that the juvenile structure and dehiscence are the same.

The elongate ovules show no distinctive characters. I have no stages in the development of seeds. The representatives of the present group studied by Peltrisot included *R. ferrugineum, R. intermedium* (*R. ferrugineum* x *hirsutum*) and *R. punctatum*. The seeds of these species are not flattened as in *Azalea* subgenus *Pentanthera*. They have scant internal integumental tissue surviving in the ends and the tails are insignificant (this would not be true in *Vireya*).

19. LEDUM L.

Ledum is a Greek word, said to designate *Cistus*, but perhaps applied also to other plants yielding odorous resins, as laurels and pistache. Linnaeus cites his predecessors as having applied such names as *Cistus, Chamaecistus, Daphne, Chamaedaphne*, and *Ledum* to various species of *Azalea, Rhododendron*, and *Kalmia*. I do not know whether he was the first to apply the name *Ledum* to

* The same type of structure occurs in *R. Dalhousiae*, an Indian species of series *Maddenii*. I have placed this series in subgenus *Rhodorastrum;* it seems to represent the transition to subgenus *Vireya*. I learn the anatomy of *R. Dalhousiae* from a paper to which Dr. Theodor Just had the kindness to call my attention: Waterston, E. J. An investigation into the leaf and flower structure of Rhododendron Griersonianum Balf. f. et Forrest, Rhododendron Dalhousiae Hook. f., and their hybrid Rhododendron Grierdal. Trans. and Proc. Bot. Soc. Edinburgh 33: 1-11. 1940. This paper shows that "*R. Grierdal*" is actually a hybrid between a lepidote *Rhododendron* and an elepidote one, i. e., a *Hymenanthes*. I would not withdraw *Hymenanthes* as a genus simply because it has been proved capable (though rarely) of hybridizing with *Rhododendron*.

a certain rhododendroid plant which is common in bogs in northern Europe. In the *Species Plantarum,* he is found so to have shifted the application of the name that it designates this species alone, as *Ledum palustre.* Of subsequently proposed species, three seem tenable, making a total of four:

I. Stamens normally ten; ovary impressed at summit.

1. LEDUM PALUSTRE L. Sp. Pl. 391. 1753. Leaves strongly revolute, ferruginous-tomentose beneath. Northern Europe and Asia, Japan, northern North America. There are several varieties.

2. LEDUM GLANDULOSUM Nuttall in Trans. Am. Phil. Soc. n. s. 8:270. 1843. Leaves plane or nearly so, glabrous (glaucous) beneath except for scattered glands. Western North America: British Columbia to California.

II. Stamens usually fewer than ten; ovary attenuate into the style.

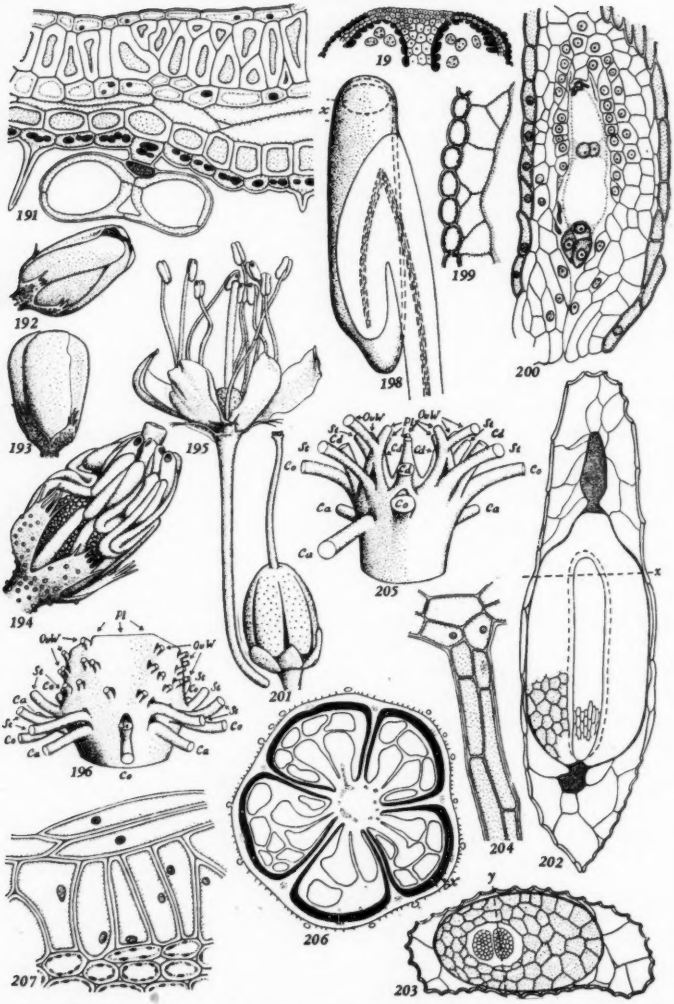
3. LEDUM GROENLANDICUM Oeder (*Ledum latifolium* Aiton; *L. candense* auctt.). Leaves strongly revolute, pale-tomentose beneath. Greenland to Alaska and south to Wisconsin and Pennsylvania.

4. LEDUM COLUMBIANUM Piper in Contrib. U. S. Nat. Herb. 11:441. 1906. Leaves strongly revolute, intensely glaucous beneath, glabrous except for scattered glands. Coastal Washington and Oregon.

For anatomical study I have material of *L. glandulosum* collected by myself both in the mountains and on the coast of northern California, and of *L. groenlandicum* collected in Ohio by Camp and near Juneau by the Juneau Botanical Club.

The plants are shrubs of moderate size, of wet habitats. They are believed to be poisonous to animals. Anderson (1), however, notes that the Eskimos make a tea from *Ledum palustre,* beside using it in medicine. Eisen (27) tells us that in Scandinavia, before the introduction of hops, the leaves were added to beer: they flavored it and enhanced the physiological effect.

The pubescence includes simple hairs of varying sizes (fig. 191). The tomentum on leaves of *L. groenlandicum* (fig. 204), and likewise, presumably, of *L. palustre,* is of multiseriate hairs not stiff enough to be called bristles. Bristles are rare, and typical glandular bristles are absent, being replaced by a characteristic modification having much in common with the glandular scales of *Rhododendron.* Each gland (figs. 189, 190, 191) stands upon a stalk, usually of just two cells placed side by side. These bear a further tier, usually of just two somewhat larger cells. This second tier is the foundation, so to speak, of the flattened-globular head, which is formed, for the rest, of a single tier, the third one, consisting of about twenty-four peculiarly modified cells. About two-thirds of them are marginally placed; these are tangentially broadened, radially flattened, and laterally in contact so as to form a cup-like structure. The remaining cells, those of the center of the tier, are tack-shaped, with the margins of their ends in contact with each other and with the marginal cells, so as to roof the cup and form a closed cavity through which their slender bodies extend. Vesque (105) took due note of these surprising structures; Breitfeld strangely failed to note the peculiarities distinguishing them from ordinary glandular bristles.



Figs. 191-203. *Ledum glandulosum*. 191. Cross section of bud scale ×320. 192, 193. Buds ×4. 194. Bud with corolla removed ×8. 195. Flower ×4. 196. Vascular system in floral receptacle ×40; labels as in fig. 29. 197. Section of young anther, cut as in fig. 176, ×160. 198. Diagram of structure of anther ×40. 199. Longitudinal section of anther wall: area marked *x* in fig. 198,× 320. 200. Longitudinal section of ovule ×320. 201. Fruit ×4. 202. Longitudinal section of seed at the plane marked *y* in fig. 203, ×80. 203. Cross section of seed at the plane marked *x* in fig. 202, × 80.

The anatomy of the stem is essentially typical of the Rhododendroideae. The pericycle consists of only one or two layers of fibers.

The leaves are essentially elliptic (often appearing linear by revolution of the margins) and rather small (rarely to 6 cm. long). Those of *L. glandulosum* (fig. 189) are about 125 μ thick. The epidermis on both sides is of small cells with a thick cuticle. The stomatal pores are bounded by inner as well as outer ridges. There are about two layers of palisade tissue, the lower exhibiting a transition to spongy tissue, the whole occupying less than half of the thickness of the leaf. The tissue above and below the veins is modified, so that these may be said to be *durchgehend*. This description agrees with Breitfeld's.

The veins form a fine network, the rectangular areas between them being measurable in tenths of a millimeter. In *groenlandicum*, the lower surfaces of these areas are strongly bowed downward, the spongy tissue in each area enclosing an extensive cavity. Sifton (92) has studied the development of these cavities. They originate soon after the leaves unfold in spring, when small numbers of cells of the spongy tissue, those which are farthest from the veins, begin to swell and to exhibit peculiarities in the staining of the cell walls. Eventually they become greatly enlarged and lose all contents, remaining only as shattered fragments of cell wall. Sifton supposes that this is a result of modified permeability, caused by the starvation of the cells farthest from the veins in leaves which are not yet self-supporting. There is evidence of the same formation of cavities in *L. glandulosum*, and I suspect that it might be found widely distributed among Rhodoreae.

The winter buds are like those of most Rhodoreae, scaly, the terminal ones mostly swollen and exclusively floriferous. Anatomically, the scales (fig. 191) may be described as differing from leaves in having a hypodermis of thick-walled fibers and a greatly reduced mesophyll.

The flowers (fig. 195) are small, white, numerous in condensed racemes or corymbs. The petals are separate. The buds (figs. 192, 193) are dorso-ventrally compressed, the corolla being narrowed at the summit to a wedge-like edge and swollen outward on the abaxial side below. The median petal is on the adaxial side; it may or may not be overlapped by the lateral petals. The normal number of stamens is ten. As anthesis approaches, the filaments become much contorted. This makes it difficult to recognize the differentiation among the stamens, which is exactly as in *Azalea* and *Rhododendron*, those of the sepalad whorl being larger than those of the petalad whorl, and those of both whorls increasing in size from the adaxial side of the flower to the abaxial. The open flowers appear actinomorphic, but the bud shows a fundamental zygomorphy.

In the floral receptacle of *L. glandulosum* (fig. 196) there is a whorl of five sepal bundles, and, above and alternating with these, a whorl of five petal bundles. The petalad stamen bundles are adnate through a short distance from their origin, to the petal bundles; the sepalad stamen bundles originate separ-

Figs. 204-207. *Ledum groenlandicum*. 204. Hair of lower surface of leaf ×320. 205. Vascular system in floral receptacle ×40; labels as in fig. 20. 206. Cross section of fruit ×16. 207. Area marked *x* in fig. 206, ×320.

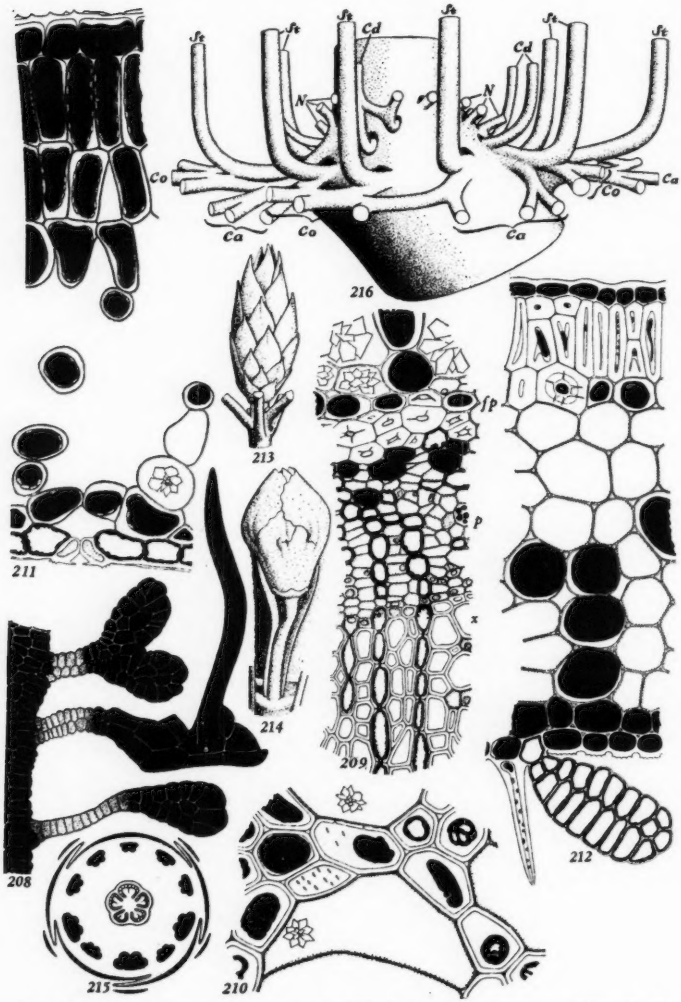


Fig. 208-216. *Hymenanthes californica*. 208. Pubescence of ovary ×160. 209. Portion of cross section of stem ×320. *fp*, fibers of pericycle; *p*, phloem; *x*, xylem. 210. Portion of cross section of pith of stem ×320. 211. Cross section of leaf ×320. 212. Cross section of bud scale ×320. 213. Floral winter bud ×0.8. 214. Flower bud from within the floral winter bud ×2. 215. Floral diagram. 216. Vascular system in floral receptacle ×20; labels as in fig. 29.

ately. Above the departure of the stamen bundles, the vascular cylinder contracts, most rapidly in the planes of the petals, so as to resemble a segment from an attenuate five-sided pyramid. Various small bundles run out above the beginning of the contraction, mostly from the angles. They supply the nectary and the ovary wall, but definite carpel dorsals are not recognizable. The style is supplied not only by some of the bundles from the ovary wall, which dip under the groove about its base to enter it, but also to some extent by bundles ascending from the central column of the ovary.

The receptacular vascular system of *L. groenlandicum* (fig. 205) differs from the one just described in a number of respects. Five sepals are present, but some of these may be completely without vascular supply. The loss of some or all of the ptalad stamens is accompanied by suppression of the corresponding bundles. There are definite carpel dorsals which ascend directly from the attenuate ovary into the style. The supply to the interior of the ovary is by five definite bundles in the planes of the sepals; from each of these there emerges a single definite ovary wall bundle which fades out at the summit of the ovary. It seems clear that the two receptacular vascular systems just described exhibit deviations from a common source; I would expect that of *L. palustre* to combine many of the primitive features of both.

The anthers are as in *Azalea* and *Rhododendron*. Dehiscence is by the collapse of a circular area of tissue, epidermal and hypodermal, the epidermal collapse tissue differing from the rest of the epidermis in being without tannin (fig. 197).

The ovule (fig. 200) is of altogether familiar type. Neither Peltrisot nor I have seen stages between ovules and ripe seeds. The latter (figs. 202, 203) are numerous, white, minute, long-tailed, the tails occupied by considerable bodies of dead and empty internal integumental cells, among which the haustoria are imbedded. The capsule (fig. 191) is exceptional in splitting from below upward.

Because of its winter buds, Maximowicz included *Ledum* among the Eurhododendreae (essentially the Rhodoreae as here limited). Because its flowers are choripetalous, Drude excluded it. The whole range of the characters of the genus shows Maximowicz to have been correct. The anthers and the symmetry of the flowers are precisely those of *Azalea, Rhododendron,* and *Hymenanthes*. If the marginal cells of the peculiar glands were radially extended, these glands would be indistinguishable from the scales of *Rhododendron*. The gross and fine structure of the leaves is altogether as in *Eurhododendron*. In aspect, inflorescence, flower buds (compare figs. 192, 193, with 184, 185), and flowers, *Ledum* resembles particularly *Rhododendron micranthum*. I am confident that this species represents essentially the ancestry of *Ledum,* and feel fortunate in having had it for study. The alternative hypothesis, that *Ledum* is ancestral to *Rhododendron,* is untenable because there is no room for *Ledum* in the obvious evolutionary sequence leading to *Rhododendron* through *Menziesia* and *Azalea*. The peculiarities of *Ledum,* choripetaly and the absence of fine filaments among the pollen tetrads, are evidently derived characters.

20. HYMENANTHES Blume

So far as I can ascertain, *Hymenanthes* Blume Bijdr. 862. 1826. is the oldest generic name applicable to the group which Rehder calls *Rhododendron* section *Leiorhodium*. It is a pleasure to take up so attractive a name as this one, which means "wedding flower": perhaps if *Hochenwartia* Crantz had been applicable to this group, I would have decided that it should not be segregated.

The original material of the genus was a cultivated plant from Japan which was peculiar in having heptamerous flowers. As a species, it was named *Hymenanthes japonica*. Subsequently, it was discovered to be an abnormal form of *Rhododendron Metternichii* S. & Z. Blume's name is older than this, but has not been transferred to *Rhododendron* and cannot be since *Azalea japonica* Gray has been. No confusion will result from the status of *Hymenanthes japonica*, alias *Rhododendron Metternichii*, as type of the genus: it belongs to the series *Ponticum*, which includes the two species of the group which were known to Linnaeus, respectively as *Rhododendron ponticum* and *R. maximum*.

Referring to *The Species of Rhododendron*, the series to be included here are *Arboreum, Auriculatum, Barbatum, Campanulatum, Falconeri, Fortunei, Fulvum, Grande, Irroratum, Lacteum, Neriiflorum, Ponticum, Taliense*, and *Thomsonii*, with a total of nearly three hundred species, beside a number of forms which are inconsistently said to be subspecies, though designated by binomial names. None of these occur in any austral land; none in the Malay region. Series *Ponticum* includes three species in North America and two in the near east; aside from these five, the genus is confined to the far east, and the overwhelming majority of the species are from the Himalayas, Burma, Tibet, Szchewan, and Yunnan.

It would be unseemly, in one who knows no more of those plants than I, to furnish new combinations wholesale. To *H. japonica* Blume and **H. pontica** (L.) comb. nov., I add names only for the species upon which I have worked and to which I must refer. Those are: **Hymenanthes californica** (Hooker) comb. nov., collected in northern California and southern Oregon by Camp, by Mrs. Dorothy Siler, and by myself; **H. maxima** (L.) comb. nov., and **H. catawbiensis** (Michaux) comb. nov., collected by Camp in the eastern United States; **H. diaprepes** (Balfour f. and W. W. Smith) comb. nov., and **H. Griersoniana** (Balfour f. and Forrest) comb. nov., both of which come from the central region of the genus, and of which material from cultivated plants was kindly furnished by the University of California Botanical Garden.

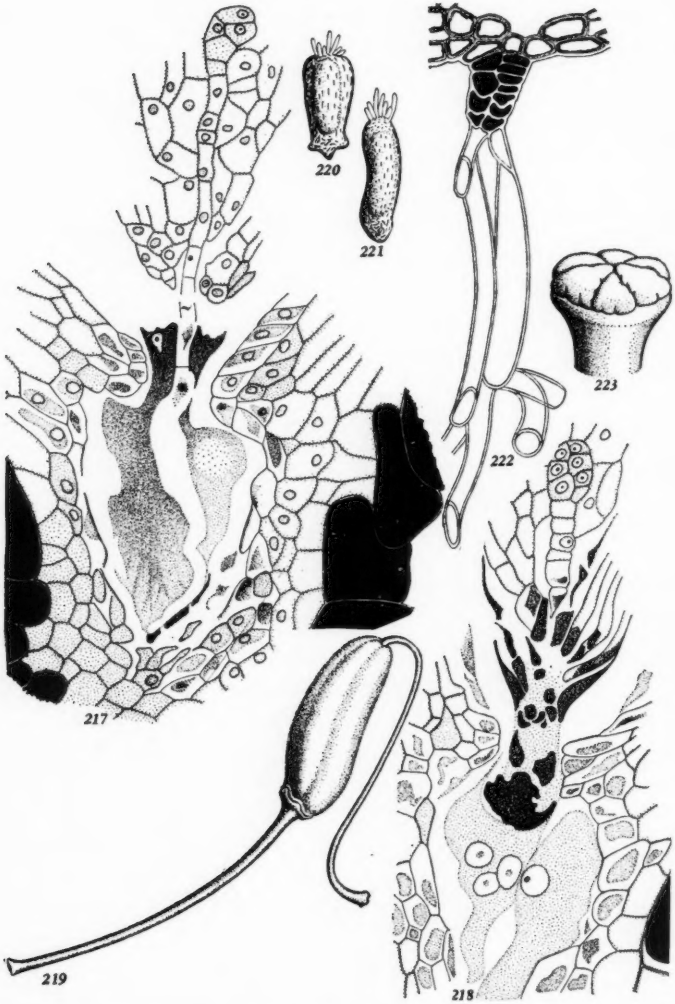
The stature of the plants is greater on the average than in *Azalea* and *Rhododendron*, sometimes recognizably arboreal. The anatomy of the stems (figs. 209, 210) is in most respects that which is typical of the Rhododendroideae. The cylinder of fibers of pericycle is not conspicuous; it consists of one or two layers of cells, and may be interrupted by gaps. In *H. diaprepes* there are bi- and tri-seriate wood rays. It is evident that these are derived, phylogenetically, from uniseriate rays: I cannot say whether they arise by the broadening of uniseriate rays, or by the squeezing out or modification of the tissue between pairs of rays.

The pubescence includes, in the first place, simple hairs (figs. 212, 225). There are multiseriate hairs of various types, sometimes straight and stiff, so as to be listed as bristles, at others branched in various fashions. The branching may be irregular (fig. 222); or the branches may be in a whorl (series *Grande*) or connate, forming goblet-like structures (series *Falconeri*) or peltate structures (figured by Breitfeld in a species of series *Ponticum*). These last are superficially similar to the scales of *Rhododendron,* and Breitfeld interprets them as comparable; to me it appears that they are modified bristles rather than modified glands. It is such hairs as these that make up the dense tomentum frequent on the lower surfaces of leaves. Typical glandular hairs, short- or long-stalked, the heads globular or elongate (fig. 212) are also present. A single structure, growing irregularly, may be partly of the character of a bristle, partly of that of a gland: such structures are abundant in the tomentum on the ovary of *H. californica* (fig. 208). Leaves which appear glabrous below may bear microscopic rudiments of glandular hairs: such is the case both in *H. californica* and *H. diaprepes* (fig. 224).

The leaves are most often lanceolate, dark-green above, laurel-like, borne on prominent stout petioles, generally large, sometimes exceding 30 cm. long. They are notably thick (figs. 211, 224), exceeding 300 μ in my specimen of *H. diaprepes,* and this is not the maximum. The epidermis if of rather small, thick-walled cells bearing a heavy cuticle on both sides. Frequently (not, I think, practically always, as implied by Breitfeld's description for *"Eurhododendron"*) the upper epidermis is underlain by a hypodermis of similar cells. Palisade tissue, of two, three, or more layers of cells, often decidedly elongate, occupies about half of the thickness of the leaf. The spongy tissue seems not well described by Breitfeld, as traversed by numerous large canals; rather, it consists of elongate cells oriented in all directions, each in contact with others at both ends, so as to form a network (regrettably, I have failed to show this well in the figures). There is evidence that the network may be formed by the enlargement of certain cells followed by their disappearance, as in *Ledum.* The veins are connected to the epidermis above and below by specialized cells, largely fibers.

The flowers emerge from enlarged terminal buds (fig. 213) which yield neither foliage leaves nor branches. The bud scales (figs. 212, 225) are of modified foliar structure, with a hypodermis of thick-walled fibers under the upper epidermis and a compact mesophyll. The inflorescences are umbelloid corymbs, usually of numerous flowers.

The ascending pedicels often enter the receptacles at such an angle that the flowers are horizontal. The flowers are usually large and always zygomorphic, with the median petal the largest and placed on the adaxial side. The number of floral leaves in each whorl is normally five. In the normal case of ten stamens being present, their pattern (fig. 215) is that which has already been described as normal for *Azalea* and *Ledum.* Multiplication of the flower parts is very common, and the various kinds of floral leaves may be variously



Figs. 217-221. *Hymenanthes californica*. 217. Micropylar portion of longitudinal section of developing seed ×320. 218. Same, a slightly later stage, ×320. 219. Fruit ×1.6. 220, 221. Seeds ×8.

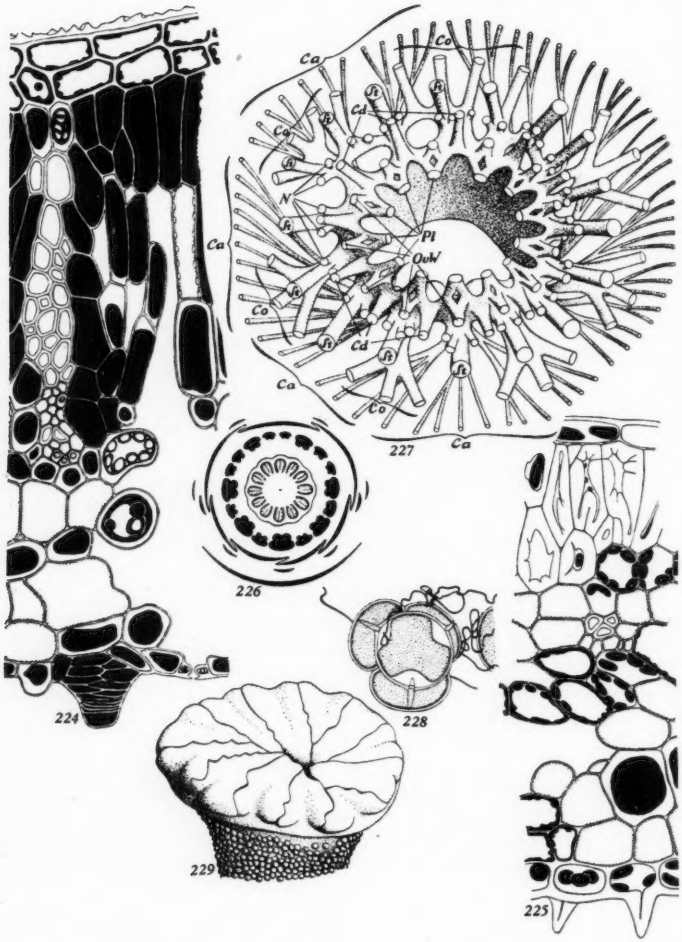
Figs. 222, 223. *Hymenanthes Griersoniana*. 222. Hair of lower surface of leaf ×320. 223. Stigma ×8.

multiplied (fig. 226 represents a flower with seven each of sepals and petals, seventeen stamens, and twelve carpels. The pattern of stamens is essentially as before, assuming a heptamerous flower; the number seventeen is reached by a doubling of some of the small petalad stamens on the upper side). Phenomena of this sort are absent except as abnormalities in *Azalea;* present but uncommon in *Rhododendron;* present in the majority of the series of *Hymenanthes.*

Hymenanthes californica has, in the floral receptacle (fig. 216), a vascular system much like that which one would construct as a prototype after noting the different types present in *Azalea* and *Azaleastrum.* The vascular cylinder expands and then contracts. Where most expanded, it emits ten bundles in the planes of the sepals and petals. These fork and anastomose, forming a more or less complete cycle of loops; each sepal is supplied by approximately three bundles descending from these, and each petal by approximately three ascending from them. The stamen bundles are adnate to the bundles leading into the loops; those to the petalad stamens are adherent through a greater distance than those to the sepalad stamens. As the vascular cylinder contracts, it emits a considerable number of rather small bundles; the lowest of these, which originate in the planes of the petals, are the carpel dorsals.

I have not illustrated the receptacular vascular system of *H. Griersoniana.* It exhibits the looping of the perianth bundles in particularly diagrammatic fashion. There are no peculiarities except such as result from the frequent presence of six carpels.

Hymenanthes diaprepes is the only species in which I have studied the vascular system in the receptacle of flowers with the parts considerably and not uniformly multiplied (fig. 227). On the abaxial side of the vascular cylinder and well below its greatest expansion, there originate three sepal bundles. These are in the positions from which the three lower sepals of a pentamerous flower would be supplied: but they branch freely, and eventually furnish practically the entire vascular supply to five sepals. Above and alternating with these calyx bundles, there originate four petal bundles which supply as many petals without contributing anything to the sepals. On the upper or adaxial side of the receptacle, at the level of the greatest expansion of the vascular cylinder, there emerge five perianth bundles; these form loops with each other before supplying, by smaller branches from below, the two upper sepals, and by larger branches from above, the three upper petals. As to stamen bundles: the petalad bundles on the abaxial side arise from the upper sides of the petal bundles; the sepalad bundles on this side arise independently at or a little above the level of the petal bundles; the stamen bundles of the adaxial side of the flower emerge from the bundles leading to the loops and (as they are more numerous than the perianth parts) from the loops themselves. Laterally with regard to the flower one finds transitions between the markedly different structures of the abaxial and adaxial sides. A large number of nectary bundles arise in the neighborhood of the bases of the stamens. Above the departure of all the perianth and stamen bundles, the vascular cylinder begins to contract



Figs. 224-229. *Hymenanthes diaprepes*. 224. Cross section of leaf ×320. 225. Cross section of bud scale ×320. 226. Floral diagram. 227. Vascular system in floral receptacle ×10; labels as in fig. 29. 228. Pollen tetrad ×320. 229. Stigma ×8.

and breaks up into alternate carpel dorsals, swinging outward, and placental bundles, swinging inward. There may be a dozen or more of each. From the outer surfaces of the placental bundles eemrge carpel laterals, which ascend the ovary walls in the planes of the septa and fade out at the summit.

I have not seen young anthers. Since mature anthers are exactly as in *Azalea, Rhododendron,* etc., it may be assumed that the juvenile structure and the dehiscence are the same.

Ovules likewise are essentially as in the related genera. Observations of developing seeds (figs. 217, 218) show stages of the typical process. Peltrisot saw mature seeds of *H. pontica* and one other species, and I have seen them only approaching maturity in *H. californica* (figs. 220, 221). There is the usual cylindrical embryo in an ellipsoid endosperm; plugs and haustoria at both ends; the haustoria lying within scant bodies of internal integumental cells which remain only as empty walls; the epidermal cells at one or both ends of the seed grown out into brief hairs, forming plumose tails.

Concluding Remarks

The use of anatomical characters in classification is no novelty. It is a matter of invoking additional characters of the same general nature as the gross characters traditionally used. Because it is somewhat arduous, it has not been very extensive; it will become more so. It will result in better knowledge of the true natural classification, which is the system that exists in nature, to be discovered, not invented or constructed. But neither these characters nor any others will yield complete knowledge of the natural system; that is something to be approached, like an asymptote, and never reached.

The taxonomic pattern formed by the living Rhododendroideae is one already familiar on a much greater scale. Tribes which are primitive, isolated, and small, precede a very extensive one, within which one can see that there are many subordinate groups whose limits and relationships can be disentangled only on the basis of detailed knowledge. This is just as in such great groups as Cormophyta, in which several minor classes precede the overwhelming group of Angiospermae, or Chordata, in which three insignificant subphyla precede Vertebrata. It is believed that this situation is neither subjective nor a coincidence, but a normal feature of natural classification.

Summary

The foregoing pages present a review of much literature on the phytography and classification of the subfamily Rhododendroideae, and of most of the literature on the antomy of the group; together with a report of original anatomical observations on material of fifteen of the twenty recognized genera.

Variation has been observed in all of the anatomical features studied. In some of them the varying characters are of little taxonomic significance: this is to say that their distribution cannot be correlated with that of other charac-

ters and that they do not serve as marks by which natural groups can be recognized. This is true, at least, of the internal structure of the young stem.

The pubescence and the internal structure of the leaf (studied particularly by Vesque and by Breitfeld), and the embryogenic process (already described particularly by Peltrisot and Samuelsson) include characters by which certain species, subgeneric groups, and genera can be recognized. The tribe Cladothamneae exhibits embryological peculiarities. For the rest, these characters do not serve for the delimitation of tribes.

Various characters of the vascular anatomy of the receptacle (here studied in this group, as it appears, for the first time) tend to mark tribes but do not serve for precise definition. Branching and anastomosing of the primary perianth bundles, with formation of loops of vascular tissue, is confined to the Rhodoreae but is not coextensive with the tribe; the origin of sepal lateral bundles from the petal bundles is usual among the Phyllodoceae, but is not universal in this group and occurs outside it in *Cladothamnus*.

Characters of the anthers (previously studied particularly by Artopoeus and by Matthews and Knox) serve for the precise delimitation of tribes. It is noteworthy that to a considerable extent the system based on these characters confirms and is confirmed by the system which Drude established on the basis of other characters.

Drude's tribe Ledeae must be abandoned, since *Ledum* is a member of a different tribe. The remaining genera which were placed here have anthers containing fine filaments among the pollen tetrads and dehiscing by means of resorption tissue. They form two tribes rather than one: Bejarieae, a single genus in which the resorption tissue is hypodermal, and Cladothamneae, four species in two genera, in which the resorption tissue involves the epidermis.

Drude's tribe Phyllodoceae is substantiated as to limits, and defined more precisely than by the characters which he used, by the presence of resorption tissue and the absence of fine filaments among the pollen tetrads. The group is of nine small and sharply separate genera, a situation indicating antiquity and much extinction.

The Rhodoreae lack resorption tissue. This character coincides in distribution with a feature of the winter buds, namely that they are protected by specialized scales, and with a feature of the floral diagram, namely that the median petal is on the adaxial side. Most members have fine filaments among the pollen tetrads. *Ledum* is definitely a member of this group, and a derived one; its peculiarities, choripetaly and the absence of fine filaments among the pollen tetrads, are derived characters.

Taxonomic changes which appear expedient are the reduction of *Tripetaleia* to *Elliottia* and of *Kalmiopsis* to *Rhodothamnus*, and the division of *Rhododendron* as currently accepted into five genera. The division is accomplished by recognition of the segregation of *Azalea*, *Azaleastrum*, and *Therorhodion*, and by the resurrection of *Hymenanthes*. Certain new combinations resulting from these changes are made.

REFERENCES

1. ANDERSON, J. P. Plants used by the Eskimo of the northern Bering Sea and arctic regions of Alaska. American Jour. Bot. **26**:714-716. 1939.

2. ARTOPOEUS, A. Über den Bau und die Öffnungsweise der Antheren und die Entwicklung der Samen der Erikaceen. Flora **92**:309-345. 1903.

3. BARNHART, J. H. The so-called generic names proposed by Ehrhart. Rhodora **20**:180-182. 1920.

4. BENTHAM, G., AND J. D. HOOKER. Genera Plantarum .... 3 vols. London. 1862-1883.

5. BERGIUS, P. J. Ledum buxifolium. Acta Acad. Petrop. **1**(1):213-214. 1778.

6. BLUME, C. L. Bijdragen tot de Flora van Nederlandsch Indië. 2 vols. Batavia. 1825-1826.

7. BONGARD, H. G. Observations sur la végétation de l'île de Sitcha. Mém. Acad. Sci. St. Pétersbourg, sér. 6, math.-phys. cl., **2**:119-177. 1833.

8. BRAUN, E. L. The red azalea of the Cumberlands. Rhodora **43**:31-36. 1941.

9. BREITFELD, A. Der anatomische Bau der Blätter der Rhododendroideae in Beziehung zu ihrer systematischen Gruppierung und zur geographischen Verbreitung. Engler's Bot. Jahrb. **9**:319-379. 1888.

10. BRIQUET, J., AND OTHERS, EDITORS. International rules of botanical nomenclature. 3d ed. Jena. 1935.

11. BROWN, N. E., AND OTHERS. Report on two botanical collections made by Messrs. F. V. McConnell and J. J. Quelch at Mount Roraima in British Guiana. Trans. Linn. Soc. Bot. **6**:1-108. 1901.

12. CAMP, W. H. Studies in the Ericales III. The genus Leiophyllum. Bull. Torrey Bot. Club **65**:99-104. 1938.

13. ———. Phyllodoce hybrids. New Flora and Silva **12**:207-211. 1940.

14. ———. Studies in the Ericales. A discussion of the genus Befaria in North America. Bull. Torrey Bot. Club **68**:100-111. 1941.

15. ——— AND A. C. SMITH. Ericaceae (in H. A. Gleason and E. P. Killip. The flora of Mount Auyan-Tepui, Venezuela). Brittonia **3**:178-185. 1939.

16. DE CANDOLLE, A. P., AND OTHERS. Prodromus systematis naturalis Regni Vegetabilis. 17 vols. Paris. 1824-1873.

17. COPELAND, H. F. Philippine Ericaceae, I: The species of Rhododendron. Philippine Jour. Sci. **40**:133-179. 1929.

18. ———. Further studies on Monotropoideae. Madroño **6**:97-119. 1941.

19. CRANTZ, H. I. N. Institutiones rei herbariae. 2 vols. Vienna. 1766.

20. DALLA TORRE, C. G., AND H. HARMS. Genera Siphonogamarum ad systema Englerianum conscripta. Leipzig. 1900-1907.

21. DESVAUX, N. A. Observations sur la famille des Rhodoracées et sur celle des Bruyères. Jour. de Bot. **1**:28-37. 1813.

22. DON, D. An attempt at a new arrangement of the Ericaceae. Edinburgh New Phil. Jour. **17**:150-160. 1834.

23. DON, G. A general system of gardening and botany. 4 vols. London. 1831-1838.

24. DOYEL, B. E. Some features of the structure of Arctostaphylos viscida. American Jour. Bot. **29**:254-259. 1942.

25. DRUDE, O. Ericaceae. in A. Engler and K. Prantl Nat. Pflanzenfam. **4**(1):15-65. 1889.

26. EICHLER, A. W. Blüthendiagramme..... 2 vols. Leipzig. 1875, 1878.

27. EISEN, G. A. in Leafl. Western Bot. **1**:95. 1934.

28. ELLIOTT, STEPHEN. A sketch of the botany of South-Carolina and Georgia. 2 vols. Charleston. 1816-1824.

29. ENDLICHER, S. Genera plantarum secundum ordines naturales disposita. Vienna. 1836-1840.

30. FEDTSCHENKO, B., AND N. BASILEVSKAJA. Revision of the genus Bejaria Mutis. Bot. Gaz. **85**:299-322. 1928.

31. FERNALD, M. L. Leiophyllum versus Dendrium. Rhodora **29**:225-227. 1927.

32. GMELIN, J. G. Flora Sibirica. 4 vols. St. Petersburg. 1747-1769.

33. GRAY, A. Chloris Boreali-Americana ..... Mem. American Acad. **3**:1-56. 1846.

34. ———. A manual of the botany of the northern United States.... Boston. 1848.

35. ———. Characters of new plants of California and elsewhere, principally of those collected by W. H. Brewer and H. N. Bolander in the State Geologic Survey. Proc. American Acad. **7**:327-344. 1868.

36. ———. Synoptical flora of North America, vol. 2, part 1. New York. 1878.

37. ———. Characteristics of the North American Flora. American Jour. Sci. and Arts, ser. 3, **28**:323-340. 1884.

38. GREENE, E. L. Novitates occidentales.—XII. Erythea **3**:62-68. 1895.

39. HAGERUP, O. Morphological and cytological studies of the Bicornes. Dansk Bot. Arkiv. **6**(1):1-26. 1928.

40. HEDWIG, R. A. Genera plantarum.... Leipzig. 1806.

41. HEGI, G. Illustrierte Flora von Mittel-Europa. 7 vols. Munich. 1906-1931.

42. HELLER, A. A. Some changes in nomenclature. Muhlenbergia **1**:1-8. 1900.

43. HENDERSON, L. F. New plants from Oregon. Rhodora **33**:203-206. 1931.

44. HOOKER, J. D. Rhododendron of Sikkim-Himalaya. London. 1849.

45. ———. Flora of British India. 7 vols. London. 1872-1897.

46. ——— AND T. THOMPSON. On Maddenia and Diplarche, new genera of Himalayan plants. Hooker's Jour. Bot. **6**:380-384. 1854.

47. HOOKER, W. J. Flora Boreali-Americana.... 2 vols. London. 1829-1840.

48. ———. Rhododendron Keysii. Bot. Mag. t. 4875. 1855.

49. HUDSON, W. Flora Anglica.... London. 1762.

50. HUNT, K. W. A study of the style and stigma, with reference to the nature of carpel. American Jour. Bot. **24**:288-294. 1937.

51. JEPSON, W. L. A flora of California, vol. 3, part 1. Berkeley, 1939.

52. JUSSIEU, A. L. Genera plantarum secundum ordines naturales disposita. Paris. 1789.

53. KLOTZSCH, J. F. Studien über die natürliche Klasse Bicornes Linné. Linnaea **24**:1-88. 1851.

54. KOCH, K. Dendrologie. . . . 3 vols. Erlangen. 1869-1873.

55. KUNZE, O. Revisio generum plantarum. . . . Würzburg. 1891-1898.

56. LINNAEUS, C. Species plantarum . . . . Stockholm. 1753.

57. ———. ———. 2d ed. Stockholm. 1762.

58. ———. Genera plantarum . . . . 6th ed. Stockholm. 1764.

59. ———. Systema Naturae. . . . 12th ed. 3 vols. Stockholm. 1766-1768.

60. LINNAEUS, C., *filius*. Mantissa plantarum altera Generum editions VI & Specierum editionis II. Stockholm. 1771.

61. MAKINO, T. Observations on the flora of Japan. Bot. Mag. Tokyo **19**:131-160. 1905.

62. MANSFELD, R., AND H. SLEUMER. Revision der Gattung Befaria Mutis. Notizbl. Bot. Gart. Berlin-Dahlem **12**:235-276. 1935.

63. MATTHEWS, J. R., AND E. M. KNOX. The comparative morphology of the stamen in the Ericaceae. Trans. and Proc. Bot. Soc. Edinburgh **29**:243-281. 1926.

64. MAXIMOWICZ, C. J. Primitiae florae Amurensis. St. Petersburg. 1859.

65. ———. Diagnoses breves plantarum novarum Japoniae et Mandschuriae, decas secunda. Bull. Acad. Sci. St. Pétersbourg **11**:429-432. 1867.

66. ———. ———, decas tertia. Op. cit. 433-439. 1867.

67. ———. Rhododendreae Asiae orientalis. Mem. Acad. Sci. St. Pétersbourg, sér. 7, vol. 16, no. 9: 1-53. 1870.

68. MEISSNER, C. F. Ericaceae. in C. F. P. Martius. Flora Brasiliensis **7**:118-181. 1863.

69. MICHAUX, A. Flora Boreali-Americana. . . . 2 vols. Paris. 1803.

70. NUTTALL, T. The genera of North American plants, and a catalogue of the species, to the year 1817. Philadelphia. 1818.

71. ———. Description and notices of new or rare plants of the natural orders Lobeliaceae, Campanulaceae, Vacciniaceae, Ericaceae, collected in a journey over the continent of North America, and during a visit to the Sandwich Islands, and Upper California. Trans. American Phil. Soc. n. s. **8**:251-272. 1843.

72. PALLAS, P. S. Flora Rossica. 2 vols. St. Petersburg. 1784, 1788.

73. PECK, M. E. Combinations proposed in "The higher plants of Oregon." Madroño **6**:133-137. 1941.

74. PELTRISOT, C. N. Développement et structure de la graine de quelques Éricacées. Note preliminaire. Jour. de Bot. **18**:234-242. 1904.

75. ———. Developpement et structure de la graine de quelques Éricacées. Jour. de Bot. **18**:309-367, 386-402. 1904.

76. PERSOON, C. H. Synopsis plantarum, seu enchiridium botanicum. . . . 2 vols. Paris.

77. PIPER, C. V. Flora of the State of Washington. Contrib. United States Nat. Herb. **11**:1-637. 1906.

78. POIRET, J. L. M. Supplément to Lamarck. Botanique. in Encyclopedie Méthodique. 5 vols. Paris. 1810-1817.

79. PURSH, F. Flora Americae Septentrionalis. 2 vols. London. 1814.

80. REHDER, A. Contributions in L. H. Bailey. Cyclopedia of American Horticulture: *Azalea*, **1**:119-123. *Bryanthus*, **1**:185-186. *Cladothamnus*, **1**:326. *Daboecia*, **1**:443. 1900. *Kalmia*, **2**:853-854. *Ledum*, **2**:895-896. *Leiophyllum*, **2**:898. *Loiseleuria*, **2**:938. 1900. *Rhododendron*, **4**:1516-1525. *Rhodothamnus*, **4**:1526. 1902.

81. ———. Contributions in L. H. Bailey. Standard Cyclopedia of Horticulture: *Azalea*, **1**:438-439. *Bryanthus*, **1**:583. 1914. *Cladothamnus*, **2**:785. *Daboecia*, **2**:950. *Elliottia*, **2**:1110. 1914. *Kalmia*, **3**:1733-1735. 1915. *Ledum*, **4**: 1833. *Leiophyllum*, **4**: 1835. *Loiseleuria*, **4**: 1902. *Menziesia*, **4**: 2037. 1916. *Phyllodoce*, **5**: 2607. *Rhododendron*, **5**:2930-2948. *Rhodothamnus*, **5**:2949. 1916. *Tripetaleia*, **6**:3382-3383. *Tsusiophyllum*, **6**:3392. 1919.

82. ———. Azalea or Loiseleuria. Jour. Arnold Arb. **2**:156-159. 1921.

83. ———. Kalmiopsis, a new genus of Ericaceae from northwest America. Jour. Arnold Arb. **13**:30-34. 1932.

84. REICHENBACH, H. G. L., EDITOR. Dr. Joh. Christ. Mössler's Handbuch der Gewächskunde . . . . . 2d ed. 3 vols. Altona. 1827-1829.

85. ———. Handbuch des natürlichen Pflanzensystems. . . . Dresden and Leipzig. 1837.

86. RYDBERG, P. A. Catalogue of the flora of Montana and the Yellowstone National Park. Mem. New York Bot. Gard. **1**:i-xi, 1-492. 1900.

87. SALISBURY, R. A. The Paradisus Londoniensis: or coloured figures of plants cultivated in the vicinity of the metroplois. . . . the figures by William Hooker. London. 1805.

88. SAMUELSSON, G. Studien über die Entwicklungsgeschichte der Blüte einiger Bicornes-Typen . . . . Svensk Bot. Tidsk. **7**:97-188. 1913.

89. SAX, K. Chromosome stability in the genus Rhododendron. American Jour. Bot. **17**:247-251. 1930.

90. SCHLECHTER, R. Die Ericaceen von Deutsch-Neu-Guinea. Engler's Bot. Jahrb. **55**:137-194. 1917-1918.

91. SIEBOLD, P. F. DE, AND J. G. ZUCCARINI. Plantarum, quas in Japonia collegit Dr. Ph. Fr. de Siebold genera nova. . . . Abh. kgl. bayerischen Akad., math.-phys. Kl., **3**:719-749. 1840.

92. SIFTON, H. B. Lysigenous air spaces in the leaf of Labrador tea, Ledum groenlandicum Oeder. New Phytologist **39**:75-79. 1940.

93. SMALL, J. K. Shrubs and trees of the southern states.—VI. Bull. Torrey Bot. Club **28**:356-361. 1901.

94. ———. Flora of the southeastern United States. New York. 1903.

95. ———. Ericales. in North American Flora **29**:1-102. 1914.

96. SMITH, J. E. Plantarum icones hactenus ineditae . . . . London. 1789-1791.

97. SOLEREDER, H. Systematic anatomy of the Dicotyledons. Translated by L. A. Boodle and F. E. Fritsch, revised by D. H. Scott. 2 vols. Oxford. 1908.

98. Species of Rhododendron, The. By H. F. Tagg, J. Hutchinson, and A. Rehder, edited by J. B. Stevenson. Edinburgh. 1930.

99. SPRAGUE, T. A. The correct spelling of certain generic names—III. Kew Bull. **1928**:337-365.

100. SPRENGEL, K. Anleitung zur Kenntniss der Gewächse. 2d ed. 2 vols. Halle. 1817, 1818.

101. ———. Caroli Linnaei Systema Vegetabilium editio decima sexta. 5 vols. Göttingen. 1825-1828.

102. STOKER, F. The genus Phyllodoce. New Flora and Silva **12**:30-42. 1939.

103. IM THURN, E., PROFESSOR OLIVER, AND OTHERS. The botany of the Roraima expedition of 1884 . . . . Trans. Linn. Soc. Bot. **2**:249-300. 1887.

104. VENTENAT, E. P. Tableau du règne végétal. 4 vols. Paris. 1794.

105. VESQUE, J. Charactères des principales familles gamopétales, tirés de l'anatomie de la feuille. Ann. Sci. Nat. Bot., sér. 7, **1**:183-360. 1885.

106. WILSON, C. L. The phylogeny of the stamen. American Jour. Bot. **24**:686-699. 1937.

107. WILSON, E. H. The rhododendrons of northeastern Asia exclusive of those belonging to the subgenus Anthodendron. Jour. Arnold Arb. **4**:33-56. 1923.

108. ——— AND A. REHDER. A monograph of azaleas. Publ. Arnold Arb. **9**:1-219. 1921.

SACRAMENTO JUNIOR COLLEGE,
SACRAMENTO, CALIF.

Flora of Jornada Experimental Range, New Mexico

Elbert L. Little, Jr., and Robert S. Campbell[1]

Contents

Introduction	626	Distinctive Species	639
Jornada Plant Collections	629	Statistical Analysis of Vegetation	643
State Records and Extensions of Range	631	Economic Aspects	649
Distribution of Species	633	Thallophyta	654
Raunkiaer's Life Forms, Classes of Leaf Size, and Cryptogam Quotients	635	Bryophyta	655
		Ferns and Seed Plants	655
		Summary	667
		References	668

Introduction

A collection of specimens of 528 species of ferns and seed plants and a few lower plants was made at Jornada Experimental Range in southern New Mexico by various members of the Forest Service during the twenty-five year period from 1915 to 1939. This local herbarium serves as a basis for an analysis of the flora and vegetation of this representative semidesert area and has contributed several interesting State records and range extensions.

Jornada Experimental Range is located in northeastern Dona Ana County with headquarters 23 miles north of Las Cruces. Occupying 302 square miles (193,394 acres), it is the largest experimental range in the United States. It lies at the southern end of Jornada del Muerto, a plain having a north-south extent of more than 100 miles.

The Spanish name Jornada del Muerto means "the day's journey of the dead man," but is sometimes translated also as "journey of death." According to Wislizenus (1848), the name refers to an old tradition that the first person who attempted to cross the plain in one day perished. At this point the banks of Rio Grande become so rough and mountainous that early travelers going north to Santa Fe were forced to leave them and journey across the desolate, waterless plain a distance of 90 miles.

It may be of interest to quote portions of an early, somewhat poetic,

---

1 Forest Service, United States Department of Agriculture, Washington, D. C. Jornada Experimental Range is a branch of the Southwestern Forest and Range Experiment Station, which is maintained by the Forest Service, United States Department of Agriculture, for the States of Arizona, New Mexico, and west Texas, with headquarters at Tucson, Arizona.

description of Jornada del Muerto by Mrs. Susan E. Wallace (1888, pp. 140-141, 143), wife of Gen. Lew Wallace, the territorial governor:

> Near the southern boundary of New Mexico the Spanish explorers were opposed by a barrier of all on earth most to be dreaded—a shadeless, waterless plateau, nearly one hundred miles long, from five to thirty miles wide, resembling the steppes of northern Asia.
>
> The portion I speak of appears to have served its time, worn out, been dispeopled and forgotten. The grass is low and mossy, with a perishing look—the shrubs, soapweed, and bony cactus writhing like some grisly skeleton; the very stones are like the scoria of a furnace. You vainly look for the flight of a bird, such as cheered the eyes of Thalaba in the desert; no bee nor fly hums in the empty air; and, save the lizard (the genius of desolation) and horn frog, there is no breath of living thing.
>
> ... Standing on the edge of the measureless waste, which is trackless as water, the first explorers might ask: "What is this strange ocean of sand, with its stillness more awful than any sea?"
>
> .... Friendly showers fall there two months in the year, and, instead of storms of rain, in spring it is burned by those of dust and sand.
>
> The spot I am trying to describe is the battleground of the elements. In winter it is made fearful by raging storms of wind and snow....
>
> In our times many a party cut off and many a traveler murdered makes good the name it bears, given by the first white men who dared its perils: *Jornada del Muerto*—"Journey of Death."

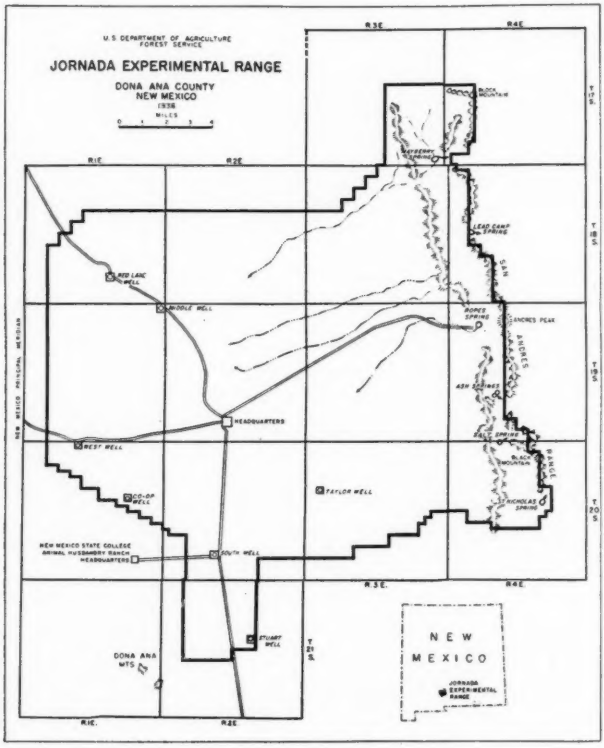
Commenting on Mrs. Wallace's description, Keyes (1905) stated that this area was considered waterless because no water appeared on the surface. He added that while abundant water lay at comparatively shallow depths, no travelers took the trouble to dig wells during nearly 350 years.

Bailey (1913) attributed the origin of the name to the death from thirst of the Spanish refugees retreating southward in 1680. He noted that in 1867 Gen. H. C. Merriam marched his infantry down this plain with only so much water as the men could carry in their canteens, covering the distance in three night marches with no great suffering or danger. Since that time the area has become occupied by cattle ranches with windmills supplying that vital resource, water. At the experimental range, water is found at depths between 300 and 350 feet.

The physiography, climate, and vegetation of Jornada Experimental Range will be reviewed briefly as a background for discussion of the flora. Three-fourths of the experimental range is within the plain of Jornada del Muerto. This portion is 10 to 20 miles east of Rio Grande, has an elevation of 4,000 to 4,600 feet, and is in the semidesert (Lower Sonoran) zone. The plain is an erosion surface formed by lateral planation and has no permanent water except wells and tanks. It is composed of unconsolidated sands, clay or adobe, and gravel of Pliocene age. The eastern quarter of the range consists of foothills and western slopes of the San Andres Mountains, which are composed chiefly of upper Paleozoic (Pennsylvanian) limestone with some sandstone and shale and which were uplifted at the close of the Tertiary. The mountains, which have a few springs, extend from the semidesert zone into the woodland (Upper

Sonoran) zone, reaching their maximum elevation of 8,000 feet on San Andreas Peak, just outside the east boundary. Their higher surfaces consist only of a western slope of bare limestone and a precipitous eastern wall. The Dona Ana Mountains, where a few of the plants were collected, are located at the southwestern edge of the Jornada Range and at one time were partly included within its boundaries. These smaller mountains consist of extrusive and intrusive igneous rocks. An account of the geology of Dona Ana County has been prepared by Dunham (1935).

The semiarid climate is characterized by the low precipitation, low humidity, hot summers, mild winters, and great daily range in temperature. Annual precipitation averages only 8.97 inches on the plain at range headquarters, elevation 4,150 feet, and 12.61 inches in the foothills at Ropes Spring, elevation 5,600 feet. About half the rainfall occurs during the summer growing



season, July, August, and September, and the remainder is fairly evenly distributed over the other months of the year. At headquarters annual average temperature is 56.3° F. and the frostless period averages 172 days. Evaporation from an open pan is very great, about 10 times the precipitation.

The vegetation of Jornada Experimental Range, which has been described by Jardine and Forsling (1922), Campbell (1929a, 1931, 1938), and others, is mainly of semidesert shrub and grassland types of the Lower Soronan zone. Vegetation maps of the area, excluding the mountain part were published by Jardine and Hurtt (1917, Fig. 2) and by Jardine and Forsling (1922, Fig. 1). Dominant species of vegetation types characterized by shrubs on the plain are honey mesquite (*Prosopis juliflora* var. *glandulosa*), broom snakeweed (*Gutierrezia sarothrae*), and soaptree yucca (*Yucca elata*) on sandy soils and sandhills; Coville creosotebush (*Larrea tridentata*) on gravelly slopes; and American tarbush or "blackbrush" (*Flourensia cernua*) on adobe. The dominant species of grassland types are black grama (*Bouteloua eriopoda*) on sands and tobosa (*Hilaria mutica*) and burrograss (*Scleropogon brevifolius*) on clay or adobe flats. Because of difference in topography and soils, the foothills have a more varied vegetation than the plain.

On the higher foothills and San Andres Mountains the shrub vegetation is of types dominated by Wright mountain-mahogany (*Cerocarpus breviflorus*), Wheeler sotol (*Dasylirion wheeleri*), and skeleton goldeneye (*Viguiera stenoloba*), and the woodland types are those characterized by pinyon (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*). A few rock plant species of the ponderosa pine (Transition) zone are represented at the summit of San Andres Peak.

Jornada Plant Collections

The work of the early botanical collectors in New Mexico has been summarized by Standley (1910a; 1910b). Blake and Atwood (1942) have listed the general and local floras of the State.

According to Standley (1910a), the first botanist to visit the interesting Jornada del Muerto was Adolf Wislizenus, who accompanied Colonel Doniphan's expedition of the Mexican War to northern Chihuahua in 1846-47. Wislizenus traveled the length of this plain during the first few days of August 1846, while en route southward from Santa Fe, and collected here the type specimens of several new species. Engelmann (Wislizenus, 1848), who made the determinations, remarked that "the famous desert, the Jornada del Muerto, furnished, as was to be expected, its quota of interesting plants." Those of the new species described from Wislizenus' specimens that have become best known include Wislizenus spectacle-pod (*Dithyrea wislizeni*), discovered near the north end of Jornada del Muerto and met with abundantly here; ocotillo (*Fouquieria splendens*); and southwest barrelcactus (*Echinocactus wislizeni*), also called "bisnaga" and Arizona water cactus, from the Dona Ana Mountains. The latter two species are characteristic and widespread in arid portions

of the Southwest. In the book describing his tour, Wislizenus (1848) recorded brief notes on the vegetation of Jornada del Muerto. He mentioned the abundance of mesquite and of "palmillas" (*Yucca elata*). The latter, the only trees he found growing on the Jornada, reached heights of 10 to 12 feet, and reminded him of African landscapes.

Several other botanists, some of them traveling with military expeditions, passed through Dona Ana, at the southern end of the plain, within the next few years.

E. O. Wooton and Paul C. Standley (1915) were located at New Mexico College of Agriculture and Mechanic Arts, only about 15 miles south of the southern boundary of what is now Jornada Experimental Range, during the years they collected in preparation for their detailed Flora of New Mexico. As a result of their extensive collections in Mesilla Valley, Organ Mountains, and southern end of Jornada del Muerto, the flora of this part of southern New Mexico is well known. In their flora the locality San Andres Mountains, including Ropes Spring, cited under more than 25 species, refers in nearly all cases to specimens collected within the present Jornada Range.

In 1912 Jornada Experimental Range was established by the Bureau of Plant Industry, United States Department of Agriculture, as Jornada Range Reserve, under the direction of Wooton. His small collections made in 1912-13 were deposited in the United States National Herbarium. From specimens collected here by Wooton in 1912, Standley (1913) described as new species *Amelanchier australis* Standl., now considered a synonym of *Amelanchier utahensis* Koehne and *Chrysothamnus elatior* Standl., later reduced to a variety, *C. pulchellus* var. *elatior* (Standl.) Kittell. In their State Flora, Wooton and Standley (1915) cited records from Jornada Range for at least two uncommon species: *Oligomeris subulata* (as *Dipetalia subulata*) and *Reverchonia arenaria.*

The present herbarium of the Jornada Experimental Range, upon which this local flora is based, was begun in 1915, when the range was transferred to the Forest Service. Specimens were collected and determined according to Forest Service instructions (1925), for the most part incidentally to regular work in grazing investigations. Collections have been forwarded to the Washington Office for determination each year, though the larger ones were made in the earlier years. After more than 20 years, specimens of additional species are still being discovered. Duplicates of more than 800 numbers representing more than 500 species of vascular plants have been deposited by the staff of the Jornada Range in the Herbarium of the Forest Service at Washington, D. C., and that at the range. These include a few specimens from the Dona Ana Mountains and the summit of San Andres Peak, both slightly outside the range boundaries.

Principal Forest Service collectors in addition to the authors are Roy H. Canfield, William R. Chapline, Robert F. Copple, Clarence L. Forsling, Ashbel F. Hough, Leon C. Hurtt, Paul B. Lister, Enoch W. Nelson, and Jacob D.

Schoeller. Credit is due these men as well as other members of the Jornada Experimental Range personnel, past and present, for their work in collecting specimens.

Mrs. K. W. Parker has kindly placed at the disposal of the authors specimens of about 20 additional species not in the Jornada herbarium. Eleven of these were from College Ranch, of New Mexico College of Agriculture and Mechanic Arts, which adjoins Jornada Experimental Range on the west.

Determinations of Jornada specimens have been made by Government specialists in the Forest Service, Bureau of Plant Industry, and National Herbarium, including among others S. F. Blake, Agnes Chase, W. A. Dayton, Doris W. Hayes, A. S. Hitchcock, William R. Maxon, Paul C. Standley, and Ivar Tidestrom. In 1939 the senior author reexamined in Washington, D. C., the entire colletcion of vascular plants with the exception of the Gramineae and brought the nomenclature up to date in accordance with the International Rules of Botanical Nomenclature and conservative trends. The nomenclature used here differs but slightly from that of Cory and Parks (1937) in their Catalogue of the Flora of Texas.

Two articles on the flora of Jornada Experimental Range have been published: a report by Canfield (1934) on a study of stem structure of grasses, listing 69 grass species, and one by Little (1937b) on a collection of bryophytes consisting of 1 liverwort and 21 moss species. The latter collection included a new species, originally described by Williams (1936) as *Moenkemeyera littlei* but now known as *Fissidens littlei* (Williams) Grout.

Since this study was made, there has appeared Tidestrom and Kittell's (1941) Flora of Arizona and New Mexico, containing additional species from New Mexico not listed by Wooton and Standley (1915). Based upon his collections in 1930, Fosberg (1931, 1940) has published an account of 18 species of Cactaceae of the Pyramid Peak region and an aestival flora of the Mesilla Valley region. Both regions are in Dona Ana County about 25 miles south of the southern boundary of Jornada Range. Another recent study of a nearby locality is that by Emerson (1935) of the vegetation of 63 species on gypsum sand dunes at White Sands National Monument. This national monument is located mostly in western Otero County with its western edge only about 5 miles from the northeastern border of Jornada Experimental Range but separated by a barrier of the San Andres Mountains. However, the nearest gypsum dunes are about 15 miles distant.

State Records and Extensions of Range

Although only a short distance away from the center of botanical exploration in New Mexico, Jornada Experimental Range has contributed several State records and various extensions of known range. However, the State records have already been reported by other workers, who have examined the Jornada specimens or have made independent collections of the same species.

Species of Jornada Experimental Range not mentioned for New Mexico by Wooton and Standley (1915) nor accounted for under other names, such as synonyms and segregates, include several records of extensions of range, recently described species, and introduced species. A list of 22 species from Jornada Range that appear to be additions to Wooton and Standley (1915) follows:

Cheilanthes wootoni Maxon
Selaginella sheldoni Maxon?
Typha angustifolia L.
Avena sativa L.
Muhlenbergia rigens (Benth.) Hitchc.
Panicum huachucae Ashe
Tragus racemosus (L.) All.
Eleocharis geniculata (L.) R. & S.
Eleocharis macrostachya Britton
Scirpus torreyi Olney?
Salix gooddingii Ball
Phoradendron cockerellii Trel.
Selenia dissecta Torr.
Dalea lemmoni Parry
Polygala longa Blake
Euphorbia parryi Engelm.
Bergia texana (Hook.) Seubert
Pinaropappus parvus Blake
Sartwellia mexicana A. Gray
Viguiera dentata (Cav.) Spreng.
Xanthium saccharatum Wallr.
Zexmenia brevifolia A. Gray

A check with Tidestrom and Kittell's (1941) recent Flora of Arizona and New Mexico was made also. Only 7 species of the Jornada flora are not included in this book nor treated apparently under other names. Of these, all are recorded from New Mexico in published records with the possible exception of *Scirpus torreyi* Olney?, the determination of which is doubtful. These additions are:

Eragrostis pilosa (L.) Beauv.
Scirpus torreyi Olney?
Phoradendron cockerellii Trel.
Selenia dissecta Torr.
Oxalis amplifolia (Trel.) Knuth
Croton fruticulosus Engelm.
Pinaropappus parvus Blake

The first record in the United States for *Sartwellia mexicana* A. Gray, of Coahuila and Zacatecas, Mexico, is a specimen from the Jornada Experimental Range cited by Fosberg and Ewan (1935). The Forest Service has an earlier collection from the same locality. The Jornada collection of *Pinaropappus parvus* at the top of San Andres Peak was the second United States record of this genus and second record of this rare species, which was discovered on the Lincoln National Forest, New Mexico, and later listed by Cory and Parks (1937) from western Texas. Dayton (1939) noted the Forest Service collections of *Selenia dissecta* Torr. in New Mexico, including three Jornada specimens. The first New Mexico collections of *Bergia texana* (Hook.) Seubert, *Zexmenia brevifolia* A. Gray, and perhaps other species of the above lists were made here. Many of the Jornada species were first records for the Herbarium of the Forest Service, but these additions were to be expected because of the great differences in flora between the semidesert range and the typical national forests in higher mountain zones.

A number of species collected on Jornada Experimental Range constitute slight extensions of range within New Mexico as recorded by Wooton and Standley (1915). Probably, however, specimens of some of these have been

found at several additional stations in the meantime, as the State has become much better explored botanically in recent years.

For the following 29 species of Jornada Range, Wooton and Standley (1915) cited only one New Mexico record. The 7 indicated by an asterisk (*) were known at that time only from the type locality.

Aristida pansa
Eragrostis pectinacea
Carex hystricina
Cladium jamaicense
**Eriogonum pannosum*
Amaranthus torreyi
**Abronia angustifolia*
Boerhaavia gracillima
Dryopetalon runcinatum
**Heuchera leptomeria?*
Astragalus subcinereus
Dalea glaberrima
**Schrankia occidentalis*
Croton fruticulosus
Cereus greggii
Mamillaria lasiacantha
Eremocarya micrantha
Salvia ramosissima
**Tetraclea angustifolia*
Tecoma stans var. *angustifolia*
Stenandrium barbatum
Houstonia fasciculata
Houstonia humifusa
**Actinea vaseyi*
Brickellia fendleri
Brickellia laciniata
Dicranocarpus parviflorus
Erigeron bellidiastrum
**Tetradymia filifolia*

The following 18 species were listed by Wooton and Standley (1915) from two or three New Mexico localities, but not from Dona Ana County. For some of them the Jornada record may represent a slight extension of known range within the State.

Notholaena fendleri
Chloris cucullata
Paspalum stramineum
Cyperus speciosus
Eleocharis rostellata
Nolina greenei
Phoradendron bolleanum
Petrophytum caespitosum
Astragalus crassicarpus
Astragalus famelicus
Astragalus pattersonii
Oxalis amplifolia
Rhamnus fasciculata
Oenothera hartwegi
Forestiera pubescens
Onosmodium molle var. *occidentale*
Physalis mollis var. *cinerascens*
Senecio riddellii

Distribution of Species

A study of the distribution of species of Jornada Experimental Range was made from data given in floras by Wooton and Standley (1915), Rydberg (1922), Standley (1920-26), Tidestrom (1925), and Hitchcock (1935). According to geographic distribution the species tend to fall into six more or less natural groups. Descriptions of these groups follow, together with abbreviations used in the list of species, examples and number of species in each, and percentages of the total 528 species. In this classification varieties were not considered, but the range of a species including its varieties was used.

1. New Mexico (NM). Species of local range known only from New Mexico. Only these 4 examples: *Schrankia occidentalis, Salvia vinacea, Actinea vaseyi,* and *Tetradymia filifolia.* 4 species, or 0.8 percent.

2. Southwestern (SW). Species occurring from western Texas to southern Arizona and northern Mexico, or extending slightly beyond these limits into southern California or in some cases to southern Utah and Nevada. These are characteristic of the semiarid Southwest (Lower Sonoran zone). Examples: *Bouteloua eriopoda, Hilaria mutica, Yucca elata, Larrea tridentata,* and *Flourensia cernua.* 228 species, or 43.2 percent.

3. Western (W). Species ranging widely through the western half of the United States, including those of Rocky Mountains and plains. Examples: *Sporobolus airoides, Atriplex canescens, Artemisia filifolia, Franseria acanthicarpa,* and *Gutierrezia sarothrae.* 216 species, or 40.9 percent.

4. North American (NA). Species distributed widely in temperate North America across the continent. A few species of this group are cosmopolitan. Examples: *Bouteloua curtipendula, Sporobolus cryptandrus,* and *Amaranthus graecizans.* 33 species, or 6.2 percent.

5. Tropical (Tr). Species of Mexico, Central America, and northern South America found northward into the southwestern States. Examples: *Andropogon saccharoides, Allionia incarnata,* and *Mollugo cerviana.* 26 species, or 4.7 percent.

6. Introduced (I). Species introduced by man or adventive from other regions. Examples: *Echinochloa crusgalli, Salsola pestifer,* and *Tribulus terrestris.* 21 species, or 4.0 percent.

The flora of Jornada Experimental Range is western and more distinctly southwestern, as more than two-fifths of the species are restricted to the southwestern semidesert area. More than two-fifths additional are western. Two species out of every five have the distribution, "western Texas to southern Arizona and northern Mexico." Texas is only about 35 miles south; Chihuahua, Mexico, about 45 miles south; and Arizona, about 125 miles west. The semidesert plain of the Lower Sonoran zone constitutes large portions of these States and has similar flora and vegetation of semidesert shrub and grassland types throughout.

A comparison of the species of the Jornada flora with Cory and Parks' (1937) catalogue of Texas plants shows that only about 59 species of the 528 are not listed from Texas or included under other names. Thus, 469 species, or 88.8 percent, of the Jornada flora extend south and southeastward across the Texas boundary, less than 50 miles distant.

Only 4 species of the Jornada list are confined within New Mexico. A few additional species listed by Wooton and Standley (1915) from New Mexico only have been recorded later by Cory and Parks (1937) from the Trans-Pecos area of western Texas. The group of southwestern species includes a few species of restricted range in southern New Mexico and western Texas also. A small list of endemic species was to be expected, because of the uniform character of topography over vast areas. *Chrysothamnus pulchellus* var. *elatior*

(Standl.) Kittell, originally described as a species, apparently is known only from the type collection at Jornada Experimental Range.

The small number of introduced species, 21, is not surprising, as the semidesert plain is sparsely inhabited, has not been under cultivation, and has no permanent water other than very limited artificial areas. Of the introduced species *Tamarix gallica* is the only shrub, and the rest are herbaceous. Thirteen are grasses, and 15 are annuals. Most of the introduced species, not being adapted to dry habitats, are confined to moist soils around wells, tanks, and mountain springs and are not commonly represented even there. Only *Salsola pestifer* and *Tribulus terrestris* are typical xerophytic species, at home away from water, and show any promise of becoming widely distributed and abundant on Jornada Range. The latter tends to spread on locally overgrazed areas, such as in the vicinity of water tanks.

Two aquatic species have an unusual disjunct occurrence at springs in San Andres Mountains. *Cladium jamaicense*, a large sedge known as Jamaica sawgrass, one of the principal species of the Florida everglades, is represented here at perhaps the third known station for New Mexico. *Typha angustifolia*, a world-wide species, was found at a salty mountain spring as probably its second record for the State.

A few of the Jornada species occur also at a great distance southward in South America. For example, *Allionia incarnata*, a common native weed here, was described by Linnaeus in 1759 from Venezuela. *Scleropogon brevifolius*, one of the commonest grasses on clay soils, escaped the notice of early collectors in the Southwest and was originally described in 1870 from Argentina.

Two widely separated semidesert areas, one in southwestern United States and northern Mexico in North America and the other in Argentina, Chile, Bolivia, and Peru in South America, have similar climates, vegetation, and floras. Standley (1916a) made a comparison of the flora of the Mesilla Valley in Dona Ana County, New Mexico, with that represented in a collection of about 300 numbers from Rio Negro in southern Argentina. He listed twenty species common to the two localities and 45 pairs of closely related species in the distant areas. Thirty-one species of weeds from the Old World adventive in the Argentinan valley are found in New Mexico also. Johnston (1940), discussing the floristic significance of the shrubs common to the North and South American deserts, has suggested that there was in the past a widely distributed American desert flora which has persisted in the southern continent but which has become greatly reduced in the northern area.

Raunkiaer's Life Forms, Classes of Leaf Size, and Cryptogam Quotients

The general habit or appearance of the flora of Jornada Experimental Range is clearly shown by a classification of the 514 species of seed plants according to Raunkiaer's (1934) life forms, which are based upon the position of the perennating buds. Life forms of the different species were determined

from field experience and herbarium specimens, supplemented by published descriptions. Each class is listed below with abbreviation, description, examples, number of species, and percentage of the total 514 species.

1. Stem succulents (S). Fleshy-stemmed plants of Jornada Range are limited to members of Cactaceae. Examples: *Echinocereus fendleri* and *Opuntia engelmannii*. 16 species, or 3.1 percent.

2. Epiphytes (E). The only vascular epiphytes here are parasitic mistletoes, family Loranthaceae. Examples: *Arceuthobium campylopodum* f. *divaricatum* and *Phoradendron cockerellii*. 4 species, or 0.8 percent.

3. Megaphanerophytes and mesophanerophytes (MM). Trees reaching heights of more than 30 meters and of 8 to 30 meters, respectively. No megaphanerophytes are present, and even along canyons and arroyos of the San Andres Mountains the only mesophanerophytes are *Populus wislizeni* and *Fraxinus velutina*. 2 species, or 0.4 percent.

4. Microphanerophytes (M). Small trees and large shrubs 2 to 8 meters tall. Found chiefly along drainage courses in mountains and foothills. Many square miles of the plain have no plants reaching the size of trees. On the plain the only common microphanerophytes are *Yucca elata, Prosopis juliflora* var. *glandulosa,* and *Rhus microphylla*. In the mountains typical microphanerophytes are *Juniperus monosperma, Pinus edulis, Quercus grisea, Garrya wrightii,* and *Chilopsis linearis*. 24 species, or 4.7 percent.

5. Nanophanerophytes (N). Shrubs less than 2 meters high, which characterize the semidesert shrub vegetation here, have a greater number of species than any other group of woody perennials. Examples: *Dasylirion wheeleri, Atriplex canescens, Cerocarpus breviflorus, Larrea tridentata, Artemisia filifolia, Flourensia cernua,* and *Viguiera stenoloba*. 64 species, or 12.4 percent.

6. Chamaephytes (Ch). Woody perennials or undershrubs with perennating buds close to the ground. These include a few composites and other plants that are woody at the base. Most common species, *Gutierrezia sarothrae*. Others: *Oenothera hartwegi, Coldenia canescens,* and *Senecio longilobus*. 21 species, or 4.1 percent.

7. Hemicryptophytes (H). Herbaceous perennials (or biennials) with perennating buds in the surface layer of soil are by far the largest group here. Examples: the grasses, *Boutelous eriopoda, Scleropogon brevifolius,* and *Sporobolus cryptandrus;* and the weeds or forbs, *Astragalus allochrous, Sphaeralcea subhastata,* and *Baileya multiradiata*. 220 species, or 42.8 percent.

8. Geophytes (G). Herbaceous perennials with buds deeply buried in the ground in rhizomes, tubers, bulbs, and roots. Examples: *Allium deserticola, Rumex hymenosepalus, Hoffmanseggia densiflora,* and *Asclepias galioides*. 19 species, or 3.7 percent.

9. Helophytes and hydrophytes (HH). Water plants and marsh plants

with buds covered by water are restricted here to springs and artificially developed water areas. Ten species of monocotyledons in the following families: Typhaceae, Najadaceae, Cyperaceae, and Juncaceae. Examples: *Typha latifolia, Eleocharis rostellata,* and *Juncus torreyi.* 10 species, or 1.9 percent.

10. Therophytes (Th). Annual herbs, of which a few appear in early spring, but most are dependent upon summer rains for growth. Common examples: *Bouteloua barbata, Eriogonum rotundifolium, Chenopodium incanum, Descurainia menziesii* var. *ochroleuca, Cryptantha crassisepala,* and *Franseria acanthicarpa.* 134 species, or 26.1 percent.

Plants of related species typically have similar life forms. However, in the genus *Houstonia* four life forms, ranging from therophytes to nanophanerophytes, are represented at Jornada Range. Three life forms are found here in the genus *Dalea* also.

A biological spectrum of the Jornada Experimental Range, consisting of percentages of various life forms among the species, is compared in Table 1 with Raunkiaer's revised normal spectrum for the earth based upon 1,000 species. When contrasted with the normal spectrum, the biological spectrum of an area is a characterization of the climate.

TABLE 1.—Comparison of biological spectrum of Jornada Experimental Range with Raunkiaer's revised normal spectrum.

Life Form	Raunkiaer's normal spectrum	Spectrum of Jornada Experimental Range
	Percent	*Percent*
Phanerophytes		
Stem succulents (S)	2	3.1
Epiphytes (E)	3	0.8
Megaphanerophytes and mesophanerophytes (MM)	8	0.4
Microphanerophytes (M)	18	4.9
Nanophanerophytes (N)	15	12.4
	46	21.6
Chamaephytes (Ch)	9	3.9
Hemicryptophytes (H)	26	42.8
Cryptophytes		
Geophytes (G)	4	3.7
Helophytes and hydrophytes (HH)	2	1.9
	6	5.6
Therophytes (Th)	13	26.1

The Jornada spectrum may not be an exact summary, as two climatic or vegetation zones are represented. However, most of the species are semidesert (Lower Sonoran). Because it has no permanent streams, also, Jornada Range

lacks many species typical of moist soils along the Rio Grande about 10 miles distant in the same zone.

Striking departures of the biological spectrum of Jornada Experimental Range from the normal spectrum are the low percentages of woody species or phanerophytes and the high percentages of herbaceous species, particularly hemicryptophytes and therophytes. All groups of phanerophytes except stem succulents are below normal, although for the nanophanerophytes, mostly semishrubs, the difference is slight. The low percentages of large phanerophytes are outstanding on this almost treeless plain. Combined percentages of megaphanerophytes, mesophanerophytes, and microphanerophytes total only one-fifth the corresponding figures of the normal spectrum.

Hemicryptophytes, which are most numerous in biological spectra of temperate regions, have the greatest excess over the percentage of the normal spectrum, and the therophytes have the next greatest. The semiarid, warm character of the climate is indicated by the high percentage of therophytes, twice the normal, and by the relatively high percentage of stem succulents. Nanophanerophytes compose the third largest group.

Approximately half the species are perennial herbs, one-fourth annual herbs, and one-fourth woody plants, mostly semidesert shrubs. Only 13 of the species of phanerophytes, or 2.5 percent of the total, have the size and habit of trees. These tree species are:

Juniperus monosperma
Pinus edulis
Yucca elata
Populus wislizeni
Salix amygdaloides var. *wrightii*
Salix exigua
Salix gooddingii
Quercus gambelii
Quercus grisea
Celtis reticulata
Morus microphylla
Prunus virens
Fraxinus velutina

Lianas are rare on the Jornada Range, and only about 15 species are listed. Herbaceous vines or twining plants are limited to 1 species of Leguminosae, *Rhynchosia texana,* and 9 additional species in the following 3 families, Asclepiadaceae, Convolvulaceae, and Cucurbitaceae. The 5 species of woody vines represented here are:

Clematis drummondii
Clematis neomexicana
Janusia gracilis
Vitis arizonica
Lonicera albiflora var. *dumosa*

The Forest Service for convenience in economic classification also divides range plants into grasses, grasslike plants (chiefly sedges and rushes), range weeds (nongrasslike herbs, or forbs), and browse plants (shrubs and trees). On this basis the flora of Jornada Experimental Range, including pteridophytes, is grouped as follows: grasses, 80 species, or 15.1 percent; grasslike plants, 11 species, or 2.1 percent; range weeds, 305 species, or 57.8 percent; and browse plants, 132 species, or 25.0 percent.

Raunkiaer (1934) has also employed classes of leaf size as a means of

preparing a biological expression for the climate and environment and as a means of comparing the vegetation of areas differing in climate. His six classes of leaf size, with the maximum area for each, are: leptophylls, 25 sq. mm.; nanophylls, 225 sq. mm.; microphylls, 2,025 sq. mm.; mesophylls, 18,225 sq. mm.; macrophylls, 164,025 sq. mm.; and megaphylls. In this classification each leaflet of a compound leaf is considered as an individual leaf.

No attempt was made to classify the species of Jornada Experimental Range as to leaf size. However, on this semidesert area where most of the plant species are xerophytes diminution in leaf surface is everywhere evident. Of the various xeromorphic adaptations exhibited, certainly the microphyllous character is the most conspicuous. Most of the species here probably would fall within the class of nanophylls, but some would be grouped as microphylls. A few, including some with scale leaves, are leptophylls, and a few are leafless most of the time.

Plants of only about 15 species at Jornada Range have large enough leaves to be classed as mesophylls. This leaf size is associated usually with compensating xeromorphic adaptations or reduction in number of leaves and in a few cases with moist habitat. The 6 species with evergreen or perennial leaves within the class of mesophylls are: *Dasylirion wheeleri, Nolina greenei, N. microcarpa, Yucca baccata, Y. elata,* and *Agave parryi.* Their leaves are either thick, elongated, and leathery or succulent. Plants of the following 9 species have deciduous or annual leaves in the class of mesophylls: *Typha angustifolia, T. latifolia, Populus wislizeni, Argemone platyceras, Vitis arizonica, Datura meteloides, Apodanthera undulata, Cucurbita foetidissima,* and *Xanthium saccharatum.* The broadleaved plants with leaves of largest size here probably are *Cucurbita foetidissima* and *Datura meteloides.*

Relative numbers of species of cryptogams likewise have been used by Raunkiaer (1934) in characterizing climates. The pteridophyte quotient of Jornada Experimental Range is 0.68; that is, the actual number of species of pteridophytes, 14, is 0.68 the number that would be normal for this area in proportion to its number of species of phanerogams or seed plants, on the basis of species of the world. Similarly, the moss quotient based upon Little's (1937b) list of 21 species and one additional species listed here, is 0.47. As only one species of liverwort was found by Little (1937b), the liverwort quotient is very low, 0.07. Thus, the semiarid climate of Jornada Experimental Range is decidedly unfavorable for mosses and liverworts and to a lesser extent unfavorable for pteridophytes. Nearly all the bryophytes and pteridophytes here are xerophytes confined to rock crevices and ledges in mountains and foothills.

Distinctive Species

A number of the species are unusual or distinctive, especially in their adaptations to the semiarid climate, and a few of these will be mentioned. Among the plants most conspicuous to the visitor is the large soaptree yucca

or "soapweed" (*Yucca elata*), which is common and widely distributed on sandy areas of black grama (*Bouteloua eriopoda*) grassland and which reaches its maximum size in this portion of southern New Mexico. An emergency feed for cattle in periods of drought and a possible source of commercial fiber, this species has been the subject of investigations by Forsling (1919) and by Campbell and Keller (1929b, 1932, 1933).

Soaptree yucca, with its usually unbranched trunk bearing terminal clusters of long, narrow, evergreen leaves, is well adapted to these dry sandy soils. Its height growth is very slow, averaging only about 1 inch a year according to measurements by Campbell and Keller. Sooner or later the trunks become so tall or branched that they lose balance and fall to the ground, but they may continue to live awhile. Then sprouts at the bases of fallen plants take their places. The usual height is 3 to 6 feet; a few individuals reach 10 or 15 feet before they die, and individuals have unbranched trunks 20 to 30 feet in height, towering above the others as landmarks visible for a distance of a mile or more. While not so spectacular as its larger relative the Joshua-tree (*Yucca brevifolia*), the soaptree yucca is equally noteworthy.

One of the largest soaptree yuccas, approximately 26½ feet in height, is shown in Fig. 1. Its unbranched woody trunk is 9 inches in diameter at the base and is mostly covered with remains of dead leaves. According to the results of the growth studies referred to above, this tree is more than 300 years old.

Yucca is the State flower of New Mexico. In late June and early July it bears clusters of large white flowers on stalks above the leaf clusters. The flowers and flower stalks are eaten by cattle. Although it produces large quantities of highly viable seed in some years, soaptree yucca reproduces almost entirely by sprouts at the bases of old plants. No seedlings in advanced stages have been discovered here.

On adobe soils perhaps the most striking plant is spiny allthorn or "crown of thorns" (*Koeberlinia spinosa*), a very spiny, much-branched shrub (Fig. 2). This is often scattered on adobe flats as the only shrub, rising above a short carpet of burrograss (*Scleropogon brevifolius*). It represents an extreme of adaptation without leaves. The branches remain green and perform the activities of photosynthesis. The bluish-black berries are eaten in great numbers by birds. This species of southwestern United States and Mexico has been found also in a limited area of Bolivia.

One species of century plant or "mescal," Parry agave or *Agave parryi* (*A. neomexicana*), is found scattered over the dry rocky slopes of San Andres Mountains (Fig. 3). *Agave neomexicana* was described originally from Organ Mountains, the adjacent range on the south, and San Andres Mountain and has a distribution southward into Texas. Probably it is not distinct from *Agave parryi*. Although the plants are below average size for *A. parryi*, they are within its size variation but grow under less precipitation than the average for that species. *Agave parryi* has a basal rosette of thick, succulent, evergreen

leaves well protected by many stout spines. At maturity there are more than 100 leaves nearly 1 foot long, forming a cluster 2 to 2½ feet in diameter. More unusual is the plant's monocarpic habit. After several years of growth a tall flower stalk is rapidly produced. The young flower stalk begins to elongate in April, and by the latter part of June, now 10 to 15 feet or more in height, it bears clusters of large yellow flowers. When the seeds have matured, the plant dies.

Among the various cacti, or stem succulents, the most distinctive is the southwest barrelcactus (*Echinocactus wislizeni*), which is not uncommon at the type locality in the Dona Ana Mountains (Fig. 4). There it grows to heights of 2 to 3½ feet and a diameter of 1½ feet. Wislizenus (1848), who

Fig. 1.—Soaptree yucca *(Yucca elata)* about 26½ feet high on Jornada Experimental Range. It is growing on a sandy area of typical black grama *(Bouteloua eriopoda)* grassland. Many smaller, average-sized soaptree yuccas appear in the background. In the distance, but within Jornada Range, is San Andres Mountain, elevation 8,000 ft.

discovered this species, reported rare specimens 3 feet and one even 4 feet in height. However, it becomes larger in Arizona, where specimens more than 6 feet high and one 11 feet high have been found.

Fig. 2.—Typical spiny allthorn bush *(Koeberlinia spinosa)* growing on an adobe flat covered by a mat of burrograss *(Scleropogon brevifolius)*. Jornada Experimental Range.

Fig. 3.—Parry agave *(Agave parryi)* in flower on rocky slope near base of the San Andres Mountains, June 19, 1935. The flower stalks are up to 16½ feet high. Other vegetation consists of semidesert shrubs of the foothills.

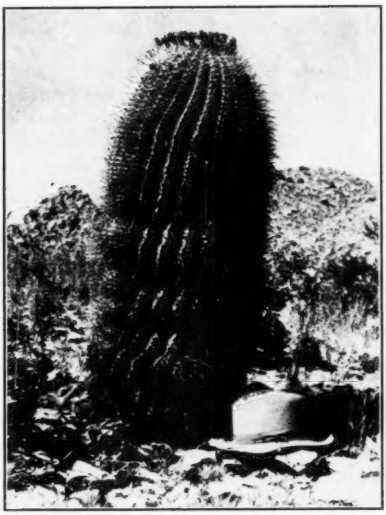


Fig. 4.—A large southwest barrelcactus *(Echinocactus wislizeni)* more than 3½ feet high, at the type locality, Dona Ana Mountains, formerly partly included in Jornada Range.

Statistical Analysis of Vegetation

The 528 species and 10 additional named varieties of pteridophytes and spermatophytes of Jornada Experimental Range are distributed among 301 genera and 82 families. The families having greatest representation, with the numbers of species in each, are: Compositae, 87; Gramineae, 80; Leguminosae, 33; Cactaceae, 16; Cruciferae, 15; and Euphorbiaceae, 15. Twenty-three families are represented by a single species each. The genera with the greatest numbers of species here are: *Muhlenbergia,* 11; *Aristida, Astragalus, Dalea,* and *Euphorbia,* 8 species each; and *Bouteloua* and *Eriogonum,* 7 each.

The greater part of the vegetation of Jornada Experimental Range is made up by relatively few dominant and common species. To determine the proportionate representation of species in the vegetation, a statistical analysis was made of data previously compiled in intensive range surveys of the area. These surveys, conducted by standard methods of the Forest Service (1932) for range reconnaissance on national forests, were made to determine the forage resources as a basis for range management. Technically trained range examiners crossed the area on foot at half-mile intervals and made detailed maps of the vegetation by subtypes, areas essentially uniform as to vegetation. For each subtype, the density of plant cover was estimated in tenths of maximum, the species making up 1 percent or more of the total composition were listed, and for each species an ocular estimate was made of the percentage of the total composition.

The plain portion of Jornada Experimental Range, containing 143,764 acres, was surveyed in 1928-29 and divided into 282 subtypes. The eastern quarter of the range, on the San Andres Mountains and foothills, known as the mountain pasture or pasture No. 11 and totaling 49,432 acres, was surveyed in 1933-34. On the latter areas, considerably more diverse in altitude, topography, and vegetation, 493 subtypes were mapped. Records from the two surveys were analyzed separately.

Data on areas occupied by plants of each species in one subtype could be obtained by multiplying the percentage of total composition of each species by both the density estimate and the acreage of the subtype. By repeating these steps for all species in all subtypes, reasonably accurate data on area occupied by plants of every species could be assembled. However, this procedure would require a great amount of calculation. A shorter, less accurate method was used in making the statistical analysis presented here. Variations in density and in area of subtypes were disregarded; all subtypes were considered as equal in extent and in density of vegetation. To a certain extent variations among subtypes as to area and density may compensate one for another, as large uniform areas of mesquite sandhills have low densities and as small types of tobosa grass have high densities.

Two values were obtained for each species: (1) the number of subtypes in which this species constitutes 0.1 percent or more of the total vegetation, and (2) the total composition of this species, determined by adding the actual percentage figures of the species for all the subtypes in which it was listed. The first value is a measure of the distribution or spread of a species on Jornada Range; the second is a measure of relative area covered by plants of this species, or a measure of the vegetation.

In a few cases different species of the same genus having the same forage value were not distinguished in the field, but were grouped together in the original field estimates. In these instances genera are included in the compilation along with species of other genera.

In the range survey of the plain portion (all Lower Sonoran) of Jornada Experimental Range the 382 subtypes were grouped into 8 general types of vegetation, having dominant species and acreages as follows:

	Acres
1. Honey mesquite *(Prosopis juliflora* var. *glandulosa)*	42,986
2. American tarbush *(Flourensia cernua)* and Coville Creosotebush *(Larrea tridentata)*	38,733
3. Black grama *(Bouteloua eriopoda)*	23,493
4. Tobosa *(Hilaria mutica)*	13,776
5. Broom snakeweed *(Gutierrezia sarothrae)*	13,509
6. Mixed grass	9,662
7. Weeds	1,335

8. Sand sagebrush *(Artemisia filifolia)*	218
Waste	52
Total	143,764

Analysis of the field records taken in the 1928-29 range survey of the plain area is summarized in Tables 2 and 3. Every species or species group making up as much as 0.1 percent, that is, one one-thousandth, of the total vegetation is listed by forage class in Table 2. The species are compared first as to the number of subtypes in which each was listed. For example, *Scleropogon brevifolius* (including *Muhlenbergia arenacea,* which is similar in appearance and is associated with the former) composed 0.1 percent or more of the stand in 208 subtypes, or 54.5 percent of the total 382 subtypes, and ranked first among the grasses in this respect.

More significant are the data on total composition. For example, *Scleropogon brevifolius* (including *Muhlenbergia arenacea*) had a total composition of 7,891, ranking first among grasses in this respect, also. This value signifies 20.9 percent of the total area covered by plants or 20.9 percent of the total volume of vegetation of all species. The figures on total composition are relative and not exact, because, as was stated above, differences in area and density of subtypes have not been taken into account.. If corrections for area and density were made, it is probable that the actual bulk of the vegetation of *Scleropogon brevifolius* and *Muhlenbergia arenacea* would be somewhat less and that of *Bouteloua eriopoda,* in second place, would be greater. In the compilation, *Scleropogon brevifolius,* which occurs in many small subtypes was overemphasized. Table 2 shows that the total composition of the vegetation of the plain area was divided among forage classes approximately as follows: grasses, 59.3 percent; browse (shrubs and trees), 33.6 percent; and weeds (forbs), 7.1 percent.

A close relation appeared between the rank of a species as to number of subtypes and its rank as to total composition. Thus, in general, the species most widely distributed over the plain area constituted the greatest percentages of its total vegetation. However, Table 2 shows several exceptions. For example, *Yucca elata* was widely distributed in almost half the subtypes but made up only 2.0 percent of the vegetation, less than certain browse species that were distributed in fewer subtypes. Conversely, weeds of a few species ranked relatively high in total composition because of their abundance in only a few subtypes.

The number of species listed is only a small fraction of the total in the flora. Although grass and browse species occupy much greater areas than do weeds, the latter include most of the species.

Table 3 lists those of the species and species groups shown in Table 2 that had a total representation of 1.0 percent or more, that is, that made up one one-hundredth or more of the total vegetation. These 13 species and groups, altogether 28 grass and browse species, composed roughly about 86.3 percent of the vegetation.

TABLE 2.—Summary of analysis of vegetation on plain portion of Jornada Range, based on 1928-29 survey, listing by forage classes every species composing 0.1 percent or more of the total vegetation.

Species	Subtype in which present		Rank as to no. of subtypes in which present	Total 1 Composition		Rank as to total composition
	Number	Percent		Number	Percent	
Total	382	100.0		38,200	100.0	
Grasses				22,611	59.3	
Scleropogon brevifolius (and *Muhlenbergia arenacea*)	208	54.5	1	7,981	20.9	1
Bouteloua eriopoda	201	52.3	2	4,557	11.9	2
Hilaria mutica	186	48.7	3	3,485	9.1	3
Sporobolus flexuosus and *S. cryptandrus*	152	39.8	4	1,584	4.1	4
Sporobolus airoides	141	36.9	5	1,290	3.4	5
Aristida spp.	110	28.8	6	1,103	2.9	6
Triodia pulchella	97	25.4	7	890	2.3	7
Annual grasses (*Bouteloua* spp. and *Aristida adscensionis*)	42	11.0	10	419	1.1	8
Muhlenbergia arenicola	56	14.7	8½	351	.9	9
Sporobolus nealleyi	6	1.6		175	.5	10
Muhlenbergia porteri	56	14.7	8½	157	.4	11
Panicum obtusum	15	3.9		98	.3	12
Triodia mutica	7	1.8		55	.1	13
Browse (shrubs and trees)				12,837	33.6	
Gutierrezia spp. (mostly *G. sarothrae*)	215	56.3	1	3,549	9.3	1
Prosopis juliflora var. *glandulosa*	175	45.8	3	2,852	7.5	2
Flourensia cernua	157	41.1	4	2,792	7.3	3
Larrea tridentata	84	22.0	5	1,706	4.5	4
Yucca elata	187	49.0	2	774	2.0	5
Atriplex canescens	34	8.9	7	263	.7	6
Artemisia filifolia	31	8.1	8	220	.6	7
Dalea scoparia	8	2.1		128	.3	8
Ephedra torreyana	53	13.9	6	125	.3	9
Lycium spp.	30	7.9	9	100	.3	10
Parthenium incanum	18	4.7	10	63	.2	11
Ephedra trifurca	17	4.5		46	.1	12
Weeds (forbs)				2,720	7.1	
Euphorbia spp.	46	12.0	4	192	.5	1
Franseria acanthicarpa	9	2.4		188	.5	2
Croton spp.	60	15.7	2	179	.5	3
Bahia absinthifolia var. *dealbata*	29	7.6	7	154	.4	4
Sida spp.	6	1.6		132	.3	5
Sphaeralcea spp.	39	10.2	5	131	.3	6
Salsola pestifer	15	3.9		127	.3	7
Perezia nana	80	20.9	1	120	.3	8
Eriogonum spp.	22	5.8		116	.3	9
Aphanostephus ramosissimus	23	6.0		111	.3	10
Hoffmanseggia spp.	24	6.3	9½	102	.3	11
Solanum elaeagnifolium	50	13.1	3	99	.3	12
Pectis spp.	38	9.9	6	96	.3	13
Boerhaavia torreyana	19	5.0		88	.2	14
Allionia incarnata	26	6.8	8	66	.2	15
Tribulus terrestris	7	1.8		46	.1	16
Cassia spp.	24	6.3	9½	43	.1	17
Amsonia arenaria	5	1.3		42	.1	18
Tidestromia lanuginosa	23	6.0		40	.1	19

1 Total of percentages of vegetation in individual subtypes.

TABLE 3.—Summary of analysis of vegetation on plain portion of Jornada Range, based on 1928-29 survey, listing every species composing 1.0 percent or more of the total vegetation.

Species	Forage class	Subtypes in which present		Rank as to no. of subtypes in which present	Total composition[1]		Rank as to total composition	Total composition classified according to grazing value of plant		
		Number	Percent		Number	Percent		High	Low	None
								Percent	Percent	Percent
Total		382	100.0		38,200	100.0				
Scleropogon brevifolius (and *Muhlenbergia arenacea*)	Grass	208	54.5	2	7,981	20.9	1		20.9	
Bouteloua eriopoda	Grass	201	52.3	3	4,557	11.9	2	11.9		
Gutierrezia spp. (mostly *G. sarothrae*)	Browse	215	56.3	1	3,549	9.3	3			9.3
Hilaria mutica	Grass	186	48.7	5	3,485	9.1	4	9.1		
Prosopis juliflora var. *glandulosa*	Browse	175	45.8	6	2,852	7.5	5		7.5	
Flourensia cernua	Browse	157	41.1	7	2,792	7.3	6			7.3
Larrea tridentata	Browse	84	22.0	12	1,706	4.5	7			4.5
Sporobolus flexuosus and *S. cryptandrus*	Grass	152	39.8	8	1,584	4.1	8	4.1		
Sporobolus airoides	Grass	141	36.9	9	1,290	3.4	9		3.4	
Aristida spp.	Grass	110	28.8	10	1,103	2.9	10	2.9		
Triodia pulchella	Grass	97	25.4	11	890	2.3	11			2.3
Yucca elata	Browse	187	49.0	4	774	2.0	12			2.0
Annual grasses (*Bouteloua* spp. and *Aristida adscensionis*)	Grass	42	11.0	20	419	1.1	13			1.1
Total of species listed					32,982	86.3		28.0	31.8	26.5

[1] Total of percentages of vegetation in individual subtypes.

Gutierrezia spp., *Scleropogon brevifolius,* and *Bouteloua eriopoda* ranked highest in number of subtypes, all being found in more than half the total number. Other species recorded in more than one-third of the subtypes were *Yucca elata, Hilaria mutica, Prosopis juliflora* var. *glandulosa, Flourensia cernua, Sporobolus flexuosus* and *S. cryptandrus,* and *S. airoides.*

In total composition *Scleropogon brevifolius* (including *Muhlenbergia arenacea*) ranked first, with 20.9 percent of all the vegetation, and *Bouteloua eriopoda* second, with 11.9 percent. Those with from 5 to 10 percent were *Gutierrezia* spp., *Hilaria mutica, Prosopis juliflora* var. *glandulosa,* and *Flourensia cernua.* All these are dominant in types occupying large areas, with the exception of *Scleropogon brevifolius,* which occurs as a dominant on clay soils in other types with *Hilaria mutica* and *Flourensia cernua.*

These species composing the bulk of the vegetation are classed in Table 3 as to forage value, the classification indicating roughly the relative proper-use factors and the rank in which the plants are preferred by grazing animals. The only common species high in forage value are *Bouteloua eriopoda, Hilaria mutica, Sporobolus flexuosus* and *S. cryptandrus,* and *Aristida* spp. The remaining common shrub and grass species are of low forage value or are not grazed. Only one of the browse species listed, *Prosopis juliflora* var. *glandulosa,* has even low forage value; the rest, with the exception of *Yucca elata,* are unpalatable or almost so. Table 3 indicates that roughly one-third of the vegetation on the plain portion of Jornada Experimental Range has high forage value, about one-third or slightly more has low forage value, and almost one-third has very slight forage value or none.

According to the range survey of 1933-34 the mountain pasture (Lower and Upper Sonoran) of 49,432 acres in the eastern part of Jornada Experimental Range was occupied by four main cover types in the following proportions: browse or shrubs, 92 percent; woodland (*Pinus edulis*), 5 percent; sand sagebrush (*Artemisia filifolia*), 1.3 percent; and grassland, 1 percent. This survey indicated that perennial grasses composed 72.3 percent of the total forage, browse 27 percent, and weeds 0.7 percent.

An analysis of the forage of the mountain pasture, made in the same manner as that for the plain area, is summarized in Tables 4 and 5. The total composition was distributed among forage classes approximately as follows: browse (shrubs and trees), 65.5 percent; grasses, 30.1 percent; weeds (forbs), 4.4 percent.

The mountain pasture had about three times as many woody species forming 0.1 percent or more of the vegetation as the plain area (Table 4). This difference is related to the greater extent of shrubby vegetation and greater diversity of topography in the mountain pasture. Here 25 species and groups, altogether 46 or fewer species, composed roughly 82.1 percent of the total vegetation.

As on the plain area, *Gutierrezia* spp. were first in number of subtypes,

with 82.2 percent, and *Bouteloua eriopoda* was second, with 75.3 percent. *Bouteloua curtipendula* was third, with 74.2 percent. The following additional species were found in more than half the subtypes: *Viguiera stenoloba, Parthenium incanum, Larrea tridentata,* and *Aristida* spp. Eleven others were represented in more than one-third of the subtypes.

In total composition *Gutierrezia* spp. were first, with 11.4 percent. Those with from 5 to 10 percent were *Bouteloua curtipendula, Larrea tridentata, Viguiera stenoloba, Bouteloua eriopoda,* and *Parthenium incanum.* Species without forage value made up a great part of the vegetation (Table 5). Among the common browse species only *Cercocarpus breviflorus* and *Dalea formosa* have high forage value for livestock and many of the shrubby species have very slight forage value or none. Probably only about one-third of the vegetation in the mountainous portion of the range has high forage value and more than half consists of unpalatable browse plants worthless as forage for livestock. However, many of these shrubby species are grazed by the abundant deer and occasional mountain sheep in the mountain area.

The statistical analysis of data from the two range surveys, besides indicating which species compose nearly all the vegetation, shows clearly that most of the semidesert species of Jornada Experimental Range are of little or no forage value and that plants palatable to livestock make up only a small part of the total.

SPRING WEEDS

The range surveys, which were made at or near the close of the summer growing season, do not show the spring weeds. For example, the weed vegetation in Table 2 is the late summer phase. In years when there is sufficient moisture, usually 1 or 2 years out of 5, perennial and annual weeds are conspicuous on Jornada Range in spring and furnish supplemental forage. More than 60 species of weeds, or forbs, were listed in the report of the spring forage crop of 1931, which was made from June 19 to July 10 of that year and shows the late spring aspect of weeds. Table 6 summarizes the records of spring weeds from that report and includes those species making up as much as 0.1 percent of the total vegetation in the spring season. However, the report was for the plain portion only and did not include the mesquite sandhill and creosotebush types. In that year the commonest species of spring annuals were *Mentzelia albicaulis* and *Eriogonum abertianum.*

Economic Aspects

The principal value of the native vegetation on semiarid upland areas in this part of southern New Mexico is as forage for livestock. On the Jornada Experimental Range and most similar areas the only kind of livestock is cattle. However, other parts of the San Andres Mountains are grazed by small herds of goats and sheep. Besides furnishing yearlong grazing for livestock, these semiarid areas support smaller numbers of native game mammals, mainly deer and antelope. A few mountain sheep, which are rare in the Southwest, live in

TABLE 4.—Summary of analysis of vegetation on Jornada mountain pasture, based on 1933-34 survey, listing every species composing 0.1 percent or more of the total vegetation.

Species	Subtypes in which present		Rank as to no. of subtypes in which present	Total [1] composition		Rank as to total composition
	Number	Percent		Number	Percent	
Total	493	100.0		49,300	100.0	
Grasses				14,829	30.1	
Bouteloua curtipendula	366	74.2	2	4,552	9.2	1
Bouteloua eriopoda	371	75.3	1	2,778	5.6	2
Bouteloua hirsuta	222	45.0	4½	1,186	2.4	3
Aristida spp.	262	53.1	3	962	2.0	4
Muhlenbergia spp.	188	38.1	6	914	1.9	5
Triodia pulchella	222	45.0	4½	856	1.7	6
Bouteloua gracilis	111	22.5	9	536	1.1	7
Eragrostis erosa	129	26.2	7	490	1.0	8
Scleropogon brevifolius	68	13.8		461	.9	9
Muhlenbergia arenacea	22	4.5		460	.9	10
Sporobolus flexuosus and *S. cryptandrus*	128	26.0	8	354	.7	11
Stipa spp.	102	20.7	10	296	.6	12
Lycurus phleoides	101	20.5		266	.5	13
Sporobolus airoides	50	10.1		198	.4	14
Hilaria mutica	20	4.1		86	.2	15
Triodia mutica	38	7.7		77	.2	16
Paspalum distichum	15	3.0		63	.1	17
Weeds (forbs)				2,148	4.4	
Aster linearis	117	23.7	1	276	.6	1
Melampodium leucanthum	44	8.9	8	151	.3	2
Eriogonum pannosum	76	15.4	3	149	.3	3
Notholaena sinuata var. *integerrima*	78	15.8	2	136	.3	4
Paronychia jamesii	53	10.8	6	134	.3	5
Actinea scaposa var. *linearis*	57	11.6	5	110	.2	6
Croton neomexicanus	50	10.1	7	98	.2	7
Perezia nana	66	13.4	4	92	.2	8
Amsonia arenaria	9	1.8		68	.1	9
Lesquerella fendleri	39	7.9	9	58	.1	10
Browse (shubs and trees)				32,208	65.5	
Gutierrezia spp. (mostly *G. sarothrae*	405	82.2	1	5,641	11.4	1
Larrea tridentata	298	60.4	4	3,642	7.4	2
Viguiera stenoloba	364	73.8	2	3,535	7.2	3
Parthenium incanum	354	71.8	3	2,519	5.1	4
Flourensia cernua	222	45.0	8	1,973	4.0	5
Cercocarpus breviflorus	130	26.4		1,854	3.8	6
Nolina greenei	179	36.3	9	1,280	2.6	7
Dasylirion wheeleri	176	35.7		1,131	2.3	8
Dalea formosa	225	45.6	7	1,041	2.1	9
Pinus edulis	72	14.6		774	1.6	10
Prosopis juliflora var. *glandulosa*	116	23.5		756	1.5	11
Ephedra torreyana	242	49.1	5	739	1.5	12
Yucca baccata	240	48.7	6	707	1.4	13
Fouquieria splendens	173	35.1		698	1.4	14

[1] Total of percentages of vegetation in individual subtypes.

TABLE 4.—(Continued) Summary of analysis of vegetation on Jornada mountain pasture, based on 1933-34 survey, listing every species composing 0.1 percent or more of the total vegetation.

Species	Subtypes in which present		Rank as to no. of subtypes in which present	Total composition		Rank as to total composition
	Number	Percent		Number	Percent	
Acacia constricta	84	17.0		694	1.4	15
Coldenia canescens	154	31.2		618	1.3	16
Dyssodia acerosa	132	26.8		563	1.1	17
Rhus spp.	178	36.1	10	550	1.1	18
Juniperus monosperma	68	13.8		406	.8	19
Condalia spathulata	69	14.0		248	.5	20
Artemisia filifolia	17	3.4		239	.5	21
Opuntia spp.	130	26.4		227	.5	22
Garrya wrightii	59	12.0		214	.4	23
Menodora scabra	110	22.3		210	.4	24
Garrya goldmanii	17	3.4		182	.4	25
Quercus gambelii	23	4.7		181	.4	26
Quercus undulata	45	9.1		177	.4	27
Astrophyllum dumosum	56	11.4		161	.3	28
Lippia wrightii	58	11.8		160	.3	29
Yucca elata	41	8.3		158	.3	30
Atriplex canescens	51	10.3		137	.3	31
Ceanothus greggii	28	5.7		105	.2	32
Fallugia paradoxa	45	9.1		103	.2	33
Agave parryi	36	7.3		63	.1	34
Unknown	18	3.7		59	.1	35
Condalia lycioides	22	4.5		54	.1	36

San Andres Mountains and are now given further protection by the establishment of the San Andres Wildlife Refuge, under the Fish and Wildlife Service.

Under a program of multiple land use, these semiarid areas have other values. A good ground cover of semidesert vegetation is useful in reducing erosion, including both wind erosion and its sandstorms and sand dunes and water erosion with flash floods which may endanger irrigated valleys below. The localities around springs in the mountains, with their groves of trees, have a high recreational value, and on Jornada Range a recreational area has been developed at Ropes Spring. The area abounds in wildlife, including such animals as mule deer, pronghorn antelope, coyotes, bobcats, jack rabbits, cottontail rabbits, numerous rodents, reptiles and amphibia (Little and Keller, 1937), birds, and occasional mountain sheep and mountain lion. There is also intermittent prospecting for oil and mineral ores. However, it is likely that in the future the economic possibilities of the semidesert plants will receive more attention and that other useful products will be made from them.

The economic importance of native western forage plants has been the subject of various investigations by the Forest Service (1914; Dayton, 1931 and 1937), and several special research projects in this field have been carried out at Jornada Experimental Range. Jardine and Forsling's (1922) investiga-

TABLE 5.—Summary of analysis of vegetation on Jornada mountain pasture, based on 1933-34 survey, listing every species composing 1.0 percent or more of the total vegetation.

Species	Forage class	Subtypes in which present		Rank as to no. of subtypes in which present	Total composition[1]		Rank as to total composition	Total composition classified according to grazing value of plant		
								High	Low	None
		Number	Percent		Number	Percent		Percent	Percent	Percent
Total		493	100.0		49,300	100.0				
Gutierrezia spp. (mostly *G. sarothrae*)	Browse	405	82.2	1	5,641	11.4	1			11.4
Bouteloua curtipendula	Grass	366	74.2	3	4,552	9.2	2	9.2		
Larrea tridentata	Browse	298	60.4	6	3,642	7.4	3			7.4
Viguiera stenoloba	Browse	364	73.8	4	3,535	7.2	4			7.2
Bouteloua eriopoda	Grass	371	75.3	2	2,778	5.6	5	5.6		
Parthenium incanum	Browse	354	71.8	5	2,519	5.1	6		5.1	
Flourensia cernua	Browse	222	45.0	12	1,973	4.0	7			4.0
Cercocarpus breviflorus	Browse	130	26.4	21½	1,854	3.8	8	3.8		
Nolina greenei	Browse	179	36.3	15	1,280	2.6	9			2.6
Bouteloua hirsuta	Grass	222	45.0	12	1,186	2.4	10	2.4		
Dasylirion wheeleri	Browse	176	35.7	17	1,131	2.3	11		2.3	
Dalea formosa	Browse	225	45.6	10	1,041	2.1	12	2.1		
Aristida spp.	Grass	262	53.1	7	962	2.0	13	2.0		
Muhlenbergia spp.	Grass	188	38.1	14	914	1.9	14	1.9		
Triodia pulchella	Grass	222	45.0	12	856	1.7	15			1.7
Pinus edulis	Browse	72	14.6	34	774	1.6	16			1.6
Prosopis juliflora var. *glandulosa*	Browse	116	23.5	26	756	1.5	17		1.5	
Ephedra torreyana	Browse	242	49.1	8	739	1.5	18		1.5	
Yucca baccata	Browse	240	48.7	9	707	1.4	19			1.4
Fouquieria splendens	Browse	173	35.1	18	698	1.4	20			1.4
Acacia constricta	Browse	84	17.0	31	694	1.4	21			1.4
Coldenia canescens	Browse	154	31.2	19	618	1.3	22			1.3
Dyssodia acerosa	Browse	132	26.8	20	563	1.1	23			1.1
Rhus spp.	Browse	178	36.1	16	550	1.1	24			1.1
Bouteloua gracilis	Grass	111	22.5	27	536	1.1	25	1.1		
Total of species listed					40,499	82.1		28.1	8.1	45.9

[1] Total of percentages of vegetation in individual subtypes.

tion of range and cattle management on southwestern ranges during drought was made here. Nelson (1934) made a study of the main forage species, black grama (*Bouteloua eriopoda*), based upon quadrat records covering a period of years; Canfield (1939) conducted a clipping study of the same species and tobosa (*Hilaria mutica*); and Campbell and Crafts (1939) prepared a leaflet on "How to keep and increase black grama on southwestern ranges."

Regarding the principal forage species here Canfield (1934) stated: "Native perennial grasses produce the major part of all the forage on Southwestern plains. In the Jornada region the species of five genera, *Bouteloua, Sporobolus, Aristida, Hilaria,* and *Scleropogon,* furnish 85 percent or more of the forage derived from grasses." According to the unpublished range survey report by E. H. Bomberger, the species of *Bouteloua* alone contribute 53.5 percent of the total forage in the Jornada mountain pasture.

Research has dealt also with range plants of negative economic importance, including those that are poisonous to livestock. Little (1937a) made a study of poisonous drymaria (*Drymaria holosteoides*), an annual weed causing

TABLE 6.—Weed species on plain portion of Jornada Range, exclusive of mesquite sandhill and creosotebush types, composing 0.1 percent or more of the spring growth of vegetation in 1931.

Species	Total composition
	Percent
Mentzelia albicaulis	2.50
Eriogonum abertianum	1.41
Croton corymbulosus	.84
Chenopodium incanum	.79
Psilostrophe tagetinae	.70
Eriogonum annuum	.65
Perezia nana	.40
Chamaesaracha coronopus	.39
Sphaeralcea spp.	.30
Lesquerella purpurea	.29
Zinnia grandiflora	.26
Hoffmanseggia spp.	.23
Allionia incarnata	.23
Cryptantha crassisepala	.22
Franseria acanthicarpa	.19
Euphorbia albomarginata	.18
Cassia bauhinioides	.16
Solanum elaeagnifolium	.16
Heliotropium convolvulaceum	.15
Eriogonum rotundifolium	.15
Baileya multiradiata	.15
Senecio longilobus	.15
Schrankia occidentalis	.14
Evolvulus pilosus	.14
Tetraclea coulteri	.12
Dithyrea wislizeni	.12
Selinocarpus chenopodioides	.11

Total of species listed ..... | 40,499 | 82.1 | | 28.1 | 8.1 | 45.9

1 Total of percentages of vegetation in individual subtypes.

greater livestock losses than all other species of poisonous range plants here. Perennial weeds regarded as poisonous are *Astragalus allochrous, A. bigelovii, Baileya multiradiata, Psilostrophe tagetinae, Senecio longilobus,* and *S. riddellii.* Other poisonous annuals are *Actinea odorata* and, in San Andres Mountains, *Nicotiana trigonophylla.* Some of these are grazed by cattle very slightly if at all, and so are less dangerous than they would be on a sheep range. Broom snakeweed (*Gutierrezia sarothrae*), an unpalatable half-shrub prominent on areas deteriorated by continued overgrazing, was studied here by Campbell and Bomberger (1934).

Since trees are scarce, the smaller woody plants are used for fuel. Larger stems and roots of *Prosopis juliflora* var. *glandulosa, Condalia spathulata,* and other shrubby species are consumed locally for this purpose. Where woodland areas are accessible, wood of *Juniperus monosperma* and *Pinus edulis* is preferred to that of semidesert shrubs for fuel. Also fence posts are made from the former.

Thallophyta

Specimens of about 16 species of thallophytes were collected at Jornada Experimental Range, mostly in connection with special studies. Although obviously very incomplete, the list of species apparently contains a few additions to New Mexico and is included here as a metter of record. The determinations were made chiefly by specialists in the Bureau of Plant Industry.

ALGAE

Nostoc commune Vauch. var. *flagelliforme* (Berk. & Curt.) Born. & Flah.

FUNGI

The small and very incomplete list of fungi collected on Jornada Experimental Range was compared with Standley's (1916b) list of the fungi of New Mexico. Standley mentioned these three parasitic species of fungi collected at Jornada Range by Wooton in 1913, including one later collected here by the Forest Service:

Albugo candida (Pers.) Roussel, on *Erysimum (Cheiniria)* sp.

Thecaphora deformans Dur. & Mont., on *Astragalus wootoni* Sheld.

Uromyces astragali Sacc., on *Astragalus wootoni* Sheld.

Three additional species from Wooton's collections in San Andres Mountains in 1912 and 1914 cited by Standley (1916b) probably came from the experimental range:

Phyllachora graminis (Pers.) Fuckel, on *Muhlenbergia pauciflora* Buckl. (*M. neomexicana* Vasey).

Puccinia aristidae Tracy, on *Aristida adscensionis* L. (*A. bromoides* H. B. K.).

Puccinia lobata Berk. & Curt., on *Sida lepidota* A. Gray (*Disella lepidota* (A. Gray) Greene).

The list of fungi collected at Jornada Experimental Range by Forest Service men follows. A majority of these, 8 species, are additions to Standley's New Mexico list and are indicated by asterisks (*).

**Batarrea stevenii* (Libosch.) Fr.
**Calvatia polygonia* Lloyd
Coprinus sp.
**Geaster coronatus* (Schaeff.) Schroet.
**Lenzites trabea* Pers.?
**Lepiota morgani* Peck.
**Montagnites candollei* Fr.
**Naucoria mexicana* Murr.?
**Phellorina strobilina* Kalchbr.

Thecaphora deformans Dur. & Mont. Smut on *Astragalus allochrous* and *A. crassicarpus*. Listed by Standley (1916b).
Tylostoma sp.
Ustilago hieronymi Schroet. Smut on *Triodia pulchella*.

LICHENES

The two named species of lichens from Jornada Range listed below were not mentioned in Lesdain's (1932) extensive report on the lichens of New Mexico. However, that study was based upon collections made by the late Brother G. Arsène in the northern part of the State.

Lecidea crenata (Tayl.) Stizenb. var. *dealbata* (Tuck.) Zahlbr.
Parmelia sp.
Ramalina populina (Ehrl.) Wainio.

Bryophyta

The bryophytes of Jornada Experimental Range, including 1 species of liverworts and 21 species of mosses, were enumerated in a separate paper by Little (1937b). A specimen of one additional moss species collected here was determined by Dr. A. J. Grout as *Weisia tortilis* (Schwaegr) C. Muell., which is rare in the United States. *Fissidens littlei* (Williams) Grout (*Moenkemeyera littlei* Williams), which has its type locality in gypsum sinks near Middle Well, Jornada Range, has been found also in Louisiana and Florida.

Ferns and Seed Plants

Each species name in the list of ferns (Pteridophyta) and seed plants (Spermatophyta) is followed by an abbreviation signifying geographical distribution or range, as discussed under the topic, Distribution of species. The abbreviations are:

NM—New Mexico	W—western	Tr—tropical
SW—southwestern	NA—North American	I—introduced

In the case of the seed plants, the first abbreviation following the name indicates the life form of the species according to Raunkiaer's classification. The standard abbreviations of Raunkiaer's life forms, which have been used here, are as follows:

S—stem succulents	Ch—chamaephytes
E—epiphytes	H—hemicryptophytes
MM—mesophanerophytes	G—geophytes
M—microphanerophytes	HH—helophytes and hydrophytes
N—nanophanerophytes	Th—therophytes

The specimens collected on the College Ranch adjacent to Jornada Experimental Range and Wooton's specimens deposited in the United States National Herbarium have been so designated in the list.

PTERIDOPHYTA

Polypodiaceae

Adiantum capillus-veneris L. Tr.
Cheilanthes feei Moore. W.
Cheilanthes villosa Davenp. SW.
Cheilanthes wootoni Maxon. W.
Notholaena fendleri Kunze. W.
Notholaena sinuata (Lag.) Kaulf. Tr.
Notholaena sinuata var. *integerrima* Hook.
Notholaena standleyi Maxon. W.
Pellaea atropurpurea (L.) Link. NA.
Pellaea intermedia Mett. SW.
Pellaea longimucronata Hook. W.
Woodsia mexicana Fée? SW.

Equisetaceae

Equisetum laevigatum A. Br. NA.

Selaginellaceae

Selaginella mutica D. C. Eaton. W.
Selaginella sheldoni Maxon ? W.

SPERMATOPHYTA
GYMNOSPERMAE
Pinaceae

Juniperus monosperma (Engelm.) Sarg. M; W.
Pinus edulis Engelm. M; W.

Ephedraceae

Ephedra aspera Engelm. N; SW.
Ephedra torreyana S. Wats. N; W.
Ephedra trifurca Torr. N; SW.

ANGIOSPERMAE
MONOCOTYLEDONEAE
Typhaceae

Typha angustifolia L. HH; NA.
Typha latifolia L. HH; NA.

Najadaceae

Potamogeton interior Rydb. HH; W.

Gramineae

Agrostis verticillata Vill. H; I.
Andropogon saccharoides Sw. H; Tr.
Aristida adscensionis L. Th; Tr.
Aristida barbata Fourn. (*A. havardii* Vasey.) H; SW.
Aristida divaricata Humb. & Bonpl. H; Tr.
Aristida glauca (Nees) Walp. H; SW.
Aristida longiseta Steud. H; W.
Aristida longiseta var. *robusta* Merr.
Aristida orcuttiana Vasey. (*A. schiediana* auth.) H; SW.
Aristida pansa Woot. & Standl. H; SW.
Aristida purpurea Nutt. H; W.
Avena sativa L. Th; I.
Bouteloua aristidoides (H. B. K.) Griseb. Th; SW.
Bouteloua barbata Lag. Th; SW.
Bouteloua curtipendula (Michx.) Torr. H; NA.
Bouteloua eriopoda (Torr.) Torr. H; SW.
Bouteloua gracilis (H. B. K.) Lag. H; W.
Bouteloua hirsuta Lag. H; W.
Bouteloua parryi (Fourn.) Griffiths. Th; SW.
Bromus catharticus Vahl. Th; I.
Cenchrus pauciflorus Benth. Th; NA.
Chloris cucullata Bisch. H; SW. College Ranch.
Chloris virgata Sw. Th. Tr.
Cynodon dactylon (L.) Pers. (*Capriola dactylon* (L). Kuntze.) H; I.
Digitaria sanguinalis (L.) Scop. Th; I.
Distichlis stricta (Torr.) Rydb. H; W.
Echinochloa crusgalli (L.) Beauv. Th; I.
Echinochloa crusgalli var. *mitis* (Pursh) Peterm.
Echinochloa crusgalli var. *zelayensis* (H. B. K.) Hitchc.
Eragrostis cilianensis (All.) Link. Th; I.
Eragrostis erosa Scribn. H; SW.
Eragrostis pectinacea (Michx.) Nees. (*E. caroliniana* (Spreng.) Scribn.) Th; NA.
Eragrostis pilosa (L.) Beauv. Th; I.
Festuca octoflora Walt. Th; NA.
Festuca octoflora var. *hirtella* Piper.

Heteropogon contortus (L.) Beauv. H; Tr.
Hilaria mutica (Buckl.) Benth. H; SW.
Koeleria cristata (L.) Pers. H; NA.
Leptochloa dubia (H. B. K.) Nees. H. Tr.
Leptochloa fascicularis (Lam.) A. Gray. Th; NA.
Leptoloma cognatum (Schult.) Chase. H; NA.
Lycurus phleoides H. B. K. H; W.
Muhlenbergia arenacea (Buckl.) Hitchc. (*Sporobolus auriculatus* Vasey.) H; SW.
Muhlenbergia arenicola Buckl. H; W.
Muhlenbergia asperifolia (Nees & Mey.) Parodi. (*Sporobolus asperifolius* (Nees & Mey.) Thurb.) H; W.
Muhlenbergia dubia Fourn. H; SW. L. N. Goodding M-286, M-287.
Muhlenbergia emersleyi Vasey. (*Epicampes emersleyi* (Vasey) Hitchc.) H; SW.
Muhlenbergia monticola Buckl. H; SW.
Muhlenbergia pauciflora Buckl. H; W.
Muhlenbergia porteri Scribn. Ch; W.
Muhlenbergia repens (Presl) Hitchc. H; SW.
Muhlenbergia rigens (Benth.) Hitchc. (*Epicampes rigens* Benth.) H; SW.
Muhlenbergia torreyi (Kunth) Hitchc. H; W. L. N. Goodding M-237.
Munroa squarrosa (Nutt.) Torr. Th; W.
Oryzopsis hymenoides (Roem. & Schult.) Ricker. H; W.
Panicum capillare L. var. *occidentale* Rydb. (*P. barbipulvinatum* Nash.) Th; NA.
Panicum hallii Vasey. H; SW.
Panicum hirticaule Presl. Th; Tr.
Panicum huachucae Ashe. H; NA.
Panicum obtusum H. B. K. H; W.
Pappophorum wrightii S. Wats. H; Tr.
Paspalum distichum L. H; NA.
Paspalum stramineum Nash. H; W.
Polypogon monspeliensis (L.) Desf. Th; I.
Scleropogon brevifolius Phil. H; W.
Setaria macrostachya H. B. K. (*Chaetochloa macrostachya* (H. B. K.) Scribn. & Merr.) H; W.
Setaria viridis (L.) Beauv. (*Chaetochloa viridis* (L.) Scribn.) Th; I.
Sitanion hystrix (Nutt.) J. G. Smith. H; W.
Sorghum halepense (L.) Pers. H; I.
Sporobolus airoides (Torr.) Torr. H; W.
Sporobolus cryptandrus (Torr.) A. Gray. H; NA.
Sporobolus flexuosus (Thurb.) Rydb. H; W.
Sporobolus giganteus Nash. H; SW.
Sporobolus nealleyi Vasey. H; SW.
Stipa columbiana Macoun. H; W.
Stipa eminens Cav. H; SW.
Stipa neomexicana (Thurb.) Scribn. H; W.
Stipa scribneri Vasey. H; W.
Tragus berteronianus Schult. (*Nazia aliena* auth.) Th; I.
Tragus racemosus (L.) All. (*Nazia racemosa* (L.) Kuntze.) Th; I.
Trichachne californica (Benth.) Chase. (*Valota saccharata* (Buckl.) Chase.) H; W.
Triodia mutica (Torr.) Scribn. H; W.
Triodia pilosa (Buckl.) Merr. H; W.
Triodia pulchella H. B. K. H; SW.

Cyperaceae

Carex hystricina Muhl. H; NA.
Cladium jamaicense Crantz. (*Mariscus jamaicensis* (Crantz) Britton.) HH; Tr.
Cyperus speciosus Vahl. Th; NA.
Cyperus uniflorus Torr. & Hook. H; SW.
Eleocharis geniculata (L.) R. & S. Th; Tr.
Eleocharis macrostachya Britton. HH; W.
Eleocharis rostellata Torr. HH; NA.

Scirpus acutus Muhl.? HH; NA.
Scirpus torreyi Olney? HH; I?

Commelinaceae

Commelina crispa Wooton. G; W.
Tradescantia occidentalis (Britton) *Smyth* var. *scopulorum* (Rose) Anderson & Woodson. (*T. scopulorum* Rose.) H; W.

Juncaceae

Juncus interior Wiegand. HH; W.
Juncus torreyi Coville. HH; NA.

Liliaceae

Allium cernuum Roth. G; NA.
Allium deserticola (Jones) Woot. & Standl. G; W.
Dasylirion wheeleri S. Wats. N; SW.
Nolina greenei S. Wats. H; W.
Nolina microcarpa S. Wats. H; SW.
Yucca baccata Torr. N; W.
Yucca elata Engelm. M; SW.

Amaryllidaceae

Agave parryi Engelm. (*A. neomexicana* Woot. & Standl.) Ch; SW.
Zephyranthes longifolia Hemsl. (*Atamosco longifolia* (Hemsl.) Cock.) G; SW.

DICOTYLEDONEAE

Salicaceae

Populus wislizeni (S. Wats.) Sarg. MM; W.
Salix amygdaloides Anderss. var. *wrightii* (Anderss.) C. Schneid. (*S. wrightii* Anderss.) M; NA.
Salix exigua Nutt. M; W.
Salix gooddingii Ball. M; SW.

Fagaceae

Quercus gambelii Nutt. (*Q. novomexicana* (A. DC.) Rydb.) M; W.
Quercus grisea Liebm. M; SW.
Quercus undulata Torr. M; W.

Ulmaceae

Celtis reticulata Torr. M; W.

Moraceae

Morus microphylla Buckl. M; SW.

Santalaceae

Comandra pallida A. DC. G; W.

Loranthaceae

Arceuthobium campylopodum Engelm. f. *divaricatum* (Engelm.) Gill. (*Razoumofskya divaricata* (Engelm.) Coville.) E; W.
Phoradendron bolleanum (Seem.) Eichl. E; SW.
Phoradendron cockerellii Trel. E; SW.
Phoradendron juniperinum Engelm. E; W.

Polygonaceae

Eriogonum abertianum Torr. Th; SW.
Eriogonum annuum Nutt. Th; W.
Eriogonum jamesii Benth. H; W.
Eriogonum pannosum Woot. & Standl. H; SW.
Eriogonum pinetorum Greene. Th; SW.
Eriogonum rotundifolium Benth. Th; SW.
Eriogonum trichopodum Torr. Th; SW.
Polygonum lapathifolium L. (*Persicaria lapathifolia* (L.) S. F. Gray.) Th; NA.
Rumex hymenosepalus Torr. G; W.
Rumex mexicanus Meisn. H; NA.

Chenopodiaceae

Atriplex canescens (Pursh) Nutt. N; W.
Chenopodium incanum (S. Wats.) Heller. Th; W.
Chenopodium leptophyllum (Moq.) Nutt. Th; W.
Corispermum nitidum Kit. Th; W.
Cycloloma atriplicifolium (Spreng.) Coult. Th; W.
Eurotia lanata (Pursh) Moq. N; W.
Salsola pestifer A. Nels. T; I.

Amaranthaceae

Acanthochiton wrightii Torr. Th; SW.
Amaranthus blitoides S. Wats. Th; W.
Amaranthus retroflexus L. Th; I.
Amaranthus torreyi (A. Gray) Benth. Th; W.
Brayulinea densa (Humb. & Bonpl.) Small. H; Tr.
Froelichia campestris Small. Th; W. College Ranch.
Tidestromia lanuginosa (Nutt.) Standl. Th; W.

Nyctaginaceae

Abronia angustifolia Greene. Th; SW.
Abronia fragrans Nutt. H; W.
Allionia incarnata L. (*Wedeliella incarnata* (L.) Cock.) H; Tr.
Allionia linearis Pursh. (*Mirabilis linearis* (Pursh) Heimerl.) H; W.
Boerhaavia caribaea Jacq. H; Tr. College Ranch.
Boerhaavia gracillima Heimerl. H; SW. College Ranch.
Boerhaavia intermedia Jones. Th; SW. College Ranch.
Boerhaavia torreyana (S. Wats.) Standl. Th; SW.
Cyphomeris gypsophiloides (Mart. & Gal.) Standl. H; SW.
Mirabilis multiflora (Torr.) A. Gray. (*Quamoclidion multiflorum* Torr.) H; W.
Selinocarpus chenopodioides A. Gray. H; SW.
Tripterocalyx cyclopterus (A. Gray) Standl. (*Abronia cycloptera* A. Gray.) Th; SW.

Illecebraceae

Paronychia jamesii Torr. & Gray. H; W.

Aizoaceae

Mollugo cerviana (L.) Seringe. Th; Tr.
Trianthema portulacastrum L. Th; Tr.

Caryophyllaceae

Drymaria holosteoides Benth. (*D. pachyphylla* Woot. & Standl.) Th; SW.
Silene laciniata Cav. H; SW.

Portulacaceae

Portulaca pilosa L. Th; Tr.
Portulaca retusa Engelm. Th; W.
Talinum angustissimum (A. Gray) Woot. & Standl. G; SW.
Talinum aurantiacum Engelm. G; SW.
Talinum pulchellum Woot. & Standl. G; SW.

Ranunculaceae

Anemone sphenophylla Poepp. G; Tr.
Aquilegia chrysantha A. Gray. H; SW.
Clematis drummondii Torr. & Gray. N; SW.
Clematis neomexicana Woot. & Standl. N; SW.
Delphinium virescens Nutt. var. *penardi* (Huth) Perry. (*D. camporum* Greene.) H; W.
Thalictrum wrightii A. Gray. H; SW.

Berberidaceae

Mahonia haematocarpa (Wooton) Fedde. (*Berberis haematocarpa* Wooton. *Odostemon haematocarpus* (Wooton) Heller.) N; SW.

Papaveraceae

Argemone platyceras Link & Otto. H; W.
Eschscholtzia mexicana Greene. Th; SW.

Fumariaceae

Corydalis montana Engelm. (*Capnoides montanum* (Engelm.) Britton.) H; W.

Cruciferae

Descurainia menziesii (DC.) O. E. Schulz var. *ochroleuca* (Wooton) O. E. Schulz. (*Sophia ochroleuca* Wooton.) Th; SW.
Dithryea wislizeni Engelm. Th; W.
Draba cuneifolia Nutt. Th; NA.
Dryopetalon runciniatum A. Gray. Th; SW.
Erysimum elatum Nutt. (*Cheirinia elata* (Nutt.) Rydb.) H; W.
Lepidium eastwoodiae Wooton. H; W.
Lepidium lasiocarpum Nutt. Th; W.
Lesquerella fendleri (A. Gray) S. Wats. H; W.
Lesquerella purpurea (A. Gray) S. Wats. H; SW.
Nerisyrenia camporum (A. Gray) Greene. H; SW.
Nerisyrenia linearifolia (S. Wats.) Greene. H; SW.
Selenia dissecta Torr. Th; SW.
Sisymbrium linearifolium (A. Gray) Payson. (*Thelypodium linearifolium* (A. Gray) S. Wats.) H; W.
Stanleyella wrightii (A. Gray) Rydb. (*Thelypodium wrightii* A. Gray.) H; W.
Streptanthus validus (Greene) Cory. (*Euklisia valida* (Greene) Woot. & Standl.) Th; SW.

Resedaceae

Oligomeris subulata (Delile) Webb. (*Dipetalia linifolia* (Vahl) Tidestrom.) Th; Tr.

Crassulaceae

Sedum griffithsii Rose. H; SW.

Saxifragaceae

Fendlera rupicola A. Gray. N; SW.
Fendlerella cymosa Greene. N; SW.
Heuchera leptomeria Greene? H; SW.
Philadelphus microphyllus A. Gray. N; W.
Ribes leptanthum A. Gray. (*Grossularia leptantha* (A. Gray) Coville & Britton.) N; W.

Rosaceae

Amelanchier utahensis Koehne. (*A. australis* Standl.) M; W. Wooton, Sept. 23, 1912 (U. S. Natl. Herb.), collected at Ropes Spring, is the type of *A. australis* Standl. Recorded by Wooton and Standley (1915, p. 323).
Cercocarpus breviflorus A. Gray. N; SW.
Fallugia paradoxa (Don) Endl. N; W.
Holodiscus dumosus (Nutt.) Heller. (*Sericotheca dumosa* (Nutt.) Rydb.) N; W.
Petrophytum caespitosum (Nutt.) Rydb. Ch; W.
Prunus virens (Woot. & Standl.) Shreve. M; SW.
Rosa neomexicana Cock. N; W.
Rosa stellata Wooton. N; SW.

Leguminosae

Acacia constricta Benth. M; SW.
Astragalus allochrous A. Gray. H; W.
Astragalus bigelovii A. Gray. H; W.
Astragalus crassicarpus Nutt. H; W.
Astragalus famelicus Sheld. H; W.
Astragalus missouriensis Nutt. H; W.
Astragalus nuttallianus DC. Th; W.
Astragalus pattersonii A. Gray. H; W.
Astragalus subcinereus A. Gray. H; SW.

Cassia bauhinioides A. Gray. H; SW.
Cassia lindheimeriana Scheele. H; SW.
Dalea formosa Torr. (*Parosela formosa* (Torr.) Vail.) N; W.
Dalea glaberrima S. Wats. (*Parosela glaberrima* (S. Wats.) Rose.) H; SW.
Dalea jamesii (Torr.) T. & G. (*Parosela jamesii* (Torr.) Vail.) H; W.
Dalea lemmoni Parry. (*Parosela lemmoni* (Parry) Heller.) Th; SW.
Dalea nana Torr. (*Parosela nana* (Torr.) Heller.) H; W.
Dalea scoparia A. Gray. (*Parosela scoparia* (A. Gray) Heller.) N; SW.
Dalea terminalis Jones. (*Parosela terminalis* (Jones) Heller.) N; SW.
Dalea wrightii A. Gray (*Parosela wrightii* (A. Gray) Vail.) H; SW.
Desmanthus cooleyi (Eaton) Trel. (*Acuan cooleyi* (Eaton) Britton & Rose.) H; W.
Hoffmanseggia densiflora Benth. G; SW.
Hoffmanseggia jamesii Torr. & Gray. G; SW.
Krameria secundiflora DC. H;
Lotus wrightii (A. Gray) Greene. H; W.
Mimosa biuncifera Benth. N; SW.
Petalostemum compactum (Spreng.) Swezey. H; W.
Phaseolus acutifolius A. Gray. Th; SW.
Prosopis juliflora var. *glandulosa* (Torr.) Cock. (*P. glandulosa* Torr.) M; W.
Prosopis pubescens Benth. (*P. odorata* Torr. & Frem.; *Strombocarpa odorata* (Torr. & Frem.) Torr.) M; SW.
Rhynchosia texana Torr. & Gray. (*Dolicholus texanus* (Torr. & Gray) Vail.) H; SW.
Robinia neomexicana A. Gray. M; W.
Schrankia occidentalis (Woot. & Standl.) Standl. (*Morongia occidentalis* Woot. & Standl.) H; NM.
Sophora stenophylla A. Gray. G; SW.

Linaceae

Linum aristatum Engelm. H; SW.
Linum australe Heller. H; W.
Linum lewisii Pursh. H; W.
Linum vernale Wooton. Th; SW.

Oxalidaceae

Oxalis amplifolia (Trel.) Knuth. G; SW.

Geraniaceae

Erodium cicutarium (L.) L'Her. Th; I.
Erodium texanum A. Gray. Th; SW.

Zygophyllaceae

Kallstroemia hirsutissima Vail. Th; W.
Larrea tridentata (DC.) Coville. (*Covillea tridentata* (DC.) Vail.) N; SW.
Tribulus terrestris L. Th; I.

Koeberliniaceae

Koeberlinia spinosa Zucc. N; SW. Also in Bolivia.

Malpighiaceae

Janusia gracilis A. Gray. N; SW.

Rutaceae

Choisya dumosa (Torr.) A. Gray. (*Astrophyllum dumosum* Torr.) N; SW.
Ptelea baldwinii Torr. & Gray. N; W.
Thamnosma texana (A. Gray) Torr. H; W.

Polygalaceae

Polygala alba Nutt. H; W.
Polygala longa Blake. H; SW.
Polygala macradenia A. Gray. Ch; SW.

Euphorbiaceae

Bernardia myricifolia (Scheele) S. Wats. N; SW.
Croton corymbulosus Engelm. H; SW.
Croton fruticulosus Engelm. N; SW.
Croton neomexicanus Muell. Arg. H; SW.
Croton texensis (Klotzsch) Muell. Arg. Th; W.
Euphorbia albomarginata Torr. & Gray. (*Chamaesyce albomarginata* (Torr. & Gray) Small.) H; W.
Euphorbia dentata Michx. (*Poinsettia dentata* (Michx.) Kl. & Garcke.) Th; NA.
Euphorbia exstipulata Engelm. (*Zygophyllidium exstipulatum* (Engelm.) Woot. & Standl.) Th; SW.
Euphorbia fendleri Torr. & Gray var. *chaetocalyx* Boiss. (*Chamaesyce chaetocalyx* (Boiss.) Woot. & Standl.) H; W.
Euphorbia hyssopifolia L. Th; Tr.
Euphorbia lata Engelm. (*Chamaesyce lata* (Engelm.) Small.) H; W.
Euphorbia parryi Engelm. (*Chamaesyce parryi* (Engelm.) Rydb.) Th; SW.
Euphorbia serpyllifolia Pers. (*Chamaesyce serpyllifolia* (Pers.) Small.) Th; W.
Reverchonia arenaria A. Gray. Th; SW.
Tragia nepetaefolia Cav. (*T. ramosa* Torr.) H; NA.

Anacardiaceae

Rhus choriophylla Woot. & Standl. N; SW.
Rhus lanceolata (A. Gray) Britton. N; SW.
Rhus microphylla Engelm. M; SW.
Rhus trilobata Nutt. N; W.
Rhus trilobata var. *pilosissima* Engler. (*R. emoryi* (Greene) Wooton.)

Sapindaceae

Sapindus drummondii Hook. & Arn. N; W.

Rhamnaceae

Ceanothus fendleri A. Gray. N; W.
Ceanothus greggii A. Gray. N; SW.
Condalia lycioides (A. Gray) Weberb. N; SW.
Condalia spathulata A. Gray. N; SW.
Rhamnus smithii Greene subsp. *fasciculata* (Greene) C. B. Wolf. (*R. fasciculata* Greene.) N; W.
Rhamnus californica Esch. subsp. *ursina* (Greene) C. B. Wolf. (*R. ursina* Greene.) M; W.

Vitaceae

Vitis arizonica Engelm. M; SW.

Malvaceae

Abutilon parvulum A. Gray. H; SW.
Hibiscus denudatus Benth. (*H. involucellatus* (A. Gray) Woot. & Standl.) Ch; SW.
Sida hastata St. Hil. (*S. physocalyx* A. Gray.) H; SW.
Sida lepidota A. Gray. H; SW.
Sida procumbens Sw. (*S. diffusa* H. B. K.) H; Tr.
Sphaeralcea coccinea (Pursh) Rydb. var. *elata* (Baker f.) Kearney. (*S. elata* (Baker f.) Rydb.) H; W.
Sphaeralcea digitata (Greene) Rydb. var. *tenuipes* (Woot. & Standl.) Kearney. (*S. tenuipes* Woot. & Standl.) H; SW.
Sphaeralcea fendleri A. Gray. H; SW.
Sphaeralcea incana Torr. H; SW.
Sphaeralcea leptophylla (A. Gray) Rydb. H; W. Wooton, May 22, 1913 (U. S. Natl. Herb.)
Sphaeralcea subhastata Coult. var. *martii* (Cock.) Kearney. H; SW.
Sphaeralcea subhastata var. *pumila* (Woot. & Standl.) Kearney. Wooton, May 17, 1913 (U. S. Natl. Herb.)

Elatinaceae

Bergia texana (Hook.) Seubert. Th; W.

Tamaricaceae

Tamarix gallica L. N; I.

Fouquieriaceae

Fouquieria splendens Engelm. M; SW.

Violaceae

Hybanthus verticillatus (Ort.) Baill. (*Calceolaria verticillata* (Ort.) Kuntze.) H; W.

Loasaceae

Cevallia sinuata Lag. H; SW.
Mentzelia albicaulis Dougl. Th; W.
Mentzelia multiflora (Nutt.) A. Gray. H; W.

Cactaceae

Cereus greggii Engelm. (*Peniocereus greggii* (Engelm.) Britt. & Rose.) S; SW.
Echinocactus horizonthalonius Lem. S; SW.
Echinocactus uncinatus Galeotti var. *wrightii* Engelm. S; SW.
Echinocactus wislizeni Engelm. S; SW.
Echinocereus coccineus Engelm. S; W.
Echinocereus fendleri (Engelm.) Rümpl. S; W.
Mammillaria heyderi Mühlenpf. C; SW.
Mammillaria lasiacantha Engelm. S; SW.
Mammillaria macromeris Engelm. (*Coryphantha macromeris* (Engelm.) Lem.) S; SW.
Mammillaria engelmannii Cory. (*M. scheeri* Mühlenpf. 1847, not 1845.) S; SW.
Mammillaria tuberculosa Engelm. S; SW.
Opuntia engelmannii Salm-Dyck. S; SW.
Opuntia imbricata (Haw.) DC. S; W.
Opuntia kleiniae DC. S; SW.
Opuntia leptocaulis DC. S; SW.
Opuntia phaeacantha Engelm.? S; W.

Lythraceae

Lythrum linearifolium (A. Gray) Small. H; SW.

Onagraceae

Gaura coccinea Pursh. H; W.
Oenothera albicaulis Pursh. (*Anogra albicaulis* (Pursh) Britton.) Th; W.
Oenothera brachycarpa A. Gray var. *wrightii* (A. Gray) Leveille (*Lavauxia wrightii* (A. Gray) Small.) H; W.
Oenothera caespitosa Nutt. var. *australis* (Woot. & Standl.) Munz. (*Pachylophus australis* Woot. & Standl.) H; W.
Oenothera caespitosa var. *marginata* (Nutt.) Munz. (*Pachylophus marginatus* (Nutt.) Rydb.)
Oenothera hartwegi Benth. (*Galpinsia hartwegi* (Benth.) Britton.) Ch; W.
Oenothera primiveris A. Gray. (*Lavauxia primiveris* (A. Gray) Small.) H; SW.
Oenothera runcinata (Engelm.) Munz. (*Anogra runcinata* (Engelm.) Woot. & Standl.) H; SW.

Umbelliferae

Pseudocymopterus montanus (A. Gray) Coult. & Rose. H; W.

Cornaceae

Garrya goldmanii Woot. & Standl. N; SW.
Garrya wrightii Torr. M; SW.

Oleaceae

Forestiera pubescens Nutt. M; W.
Fraxinus velutina Torr. MM; SW.
Fraxinus cuspidata Torr. N; SW.
Menodora scabra A. Gray. Ch; SW.

Apocynaceae

Amsonia arenaria Standl. G; SW.

Asclepiadaceae

Asclepias arenaria Torr. H; SW.
Asclepias brachystephana Engelm. H; W.
Asclepias galioides H. B. K. G; W.
Asclepiodora decumbens (Nutt.) A. Gray. H; W.
Funastrum heterophyllum (Engelm). Standl. H; SW.
Vincetoxicum productum (Torr.) Vail. H; SW.

Convolvulaceae

Convolvulus incanus Vahl. H; W. College Ranch.
Cuscuta umbellata H. B. K. Th; Tr.
Evolvulus pilosus Nutt. H; W.
Ipomoea costellata Torr. Th; SW.
Ipomoea hirsutula Jacq. f. Th; SW.

Polemoniaceae

Gilia aggregata (Pursh) Spreng. H; W.
Gilia filifolia Nutt. (*Welwitschia filifolia* (Nutt.) Rydb.) Th; W.
Gilia longiflora (Torr.) Don. Th; W.
Gilia pumila Nutt. Th; W.
Phlox stansburyi (Torr.) Heller. H; SW.
Phlox triovulata Thurb. H; SW.

Hydrophyllaceae

Nama dichotomum (Ruiz & Pavon) Choisy? (*Conanthus angustifolius* (A. Gray) Heller?) Th; W.
Nama hispidum A. Gray. (*Conanthus hispidus* (A. Gray) Heller.) Th; SW.
Phacelia intermedia Wooton. Th; SW.
Phacelia popei Torr. & Gray. Th; SW.
Phacelia rupestris Greene. H; SW.

Boraginaceae

Coldenia canescens DC. Ch; SW.
Cryptanthe crassisepala (Torr. & Gray) Greene. Th; W.
Cryptantha jamesii (Torr.) Payson. (*Oreocarya suffruticosa* (Torr.) Greene.) H; W.
Cryptantha micrantha (Torr.) Johnston. (*Eremocarya micrantha* (Torr.) Greene.) Th; W.
Cryptantha oblata (James) Payson. H; SW.
Heliotropium convolvulaceum (Nutt.) A. Gray. (*Euploca convolvulacea* Nutt.) Th; W.
Heliotropium curassavicum L. Th; NA.
Heliotropium greggii Torr. H; SW.
Lithospermum incisum Lehm. (*L. linearifolium* Goldie.) H; W.
Onosmodium molle Michx. var. *occidentale* (Mackenzie) Johnston. (*O. occidentale* Mackenzie.) H; W.

Verbenaceae

Lippia wrightii A. Gray. N; SW.
Verbena bracteata Lag. & Rodr. H; NA.
Verbena wrightii A. Gray. (*V. ambrosifolia* Rydb.) H; SW.

Labiatae

Agastache cana (Hook.) Woot. & Standl. H; SW.
Hedeoma drummondii Benth. H; W.
Hedeoma nanum (Torr.) Briq. H; SW.
Hedeoma oblongifolium (A. Gray) Heller. H; SW.
Salvia henryi A. Gray. Wooton, May 23, 1913 (U. S. Natl. Herb.)
Salvia lanceaefolia Poir. Th; W.
Salvia ramosissima Fernald. N; SW.

Salvia vinacea Woot. & Standl. N; NM.
Tetraclea angustifolia Woot. & Standl. H; SW.
Tetraclea coulteri A. Gray. H; SW.

Solanaceae

Chamaesaracha coronopus (Dunal) A. Gray. H; W.
Chamaesaracha sordida (Dunal) A. Gray. (*C. conioides* (Moric.) Britton.) H; W.
Datura meteloides DC. H; W.
Lycium berlandieri Dunal. N; SW.
Lycium pallidum Miers. N; W.
Nicotiana trigonophylla Dunal. Th; W.
Physalis hederaefolia A. Gray. H; W.
Physalis mollis Nutt. var. *cinerascens* (Dunal) A. Gray. H; W. College Ranch.
Solanum citrullifolium A. Br. (*S. heterodoxum* auth.) Th; W.
Solanum elaeagnifolium Cav. H; W.
Solanum jamesii Torr. G; W.
Solanum rostratum Dunal. Th; W.

Scrophulariaceae

Castilleja integra A. Gray. H; W.
Castilleja lanata A. Gray. H; SW.
Castilleja sessiliflora Pursh. H; W.
Cordylanthus wrightii A. Gray. (*Adenostegia wrightii* (A. Gray) Greene.) Th; W.
Maurandya antirrhiniflora Humb. & Bonpl. (*Antirrhinum antirrhiniflorum* (Humb. & Bonpl.) Hitchc.) Th; SW.
Maurandya wislizeni A. Gray. Th; SW.
Mimulus guttatus DC. (*M. cordatus* Greene.) Th; W.
Penstemon ambiguus Torr. H; W.
Penstemon fendleri A. Gray. H; W.
Penstemon torreyi Benth. H; W.

Orobanchaceae

Conopholis mexicana A. Gray. G; SW.
Orobanche multiflora Nutt. G; W.

Bignoniaceae

Chilopsis linearis (Cav.) Sweet. M; SW.
Tecoma stans (L.) Juss. var. *angustifolia* Rehd. (*Stenolobium incisum* Rose & Standl.) N; Tr.

Martyniaceae

Proboscidea arenaria (Engelm.) Decne. (*Martynia arenaria* Engelm.) Th; W.
Proboscidea parviflora (Wooton) Woot. & Standl. (*Martynia parviflora* Wooton) Th; W.

Acanthaceae

Carlowrightia linearifolia (Torr.) A. Gray. Ch; SW. College Ranch.
Stenandrium barbatum Torr. & Gray. H; SW.

Plantaginaceae

Plantago major L. H; I.
Plantago purshii Roem. & Schult. Th; W.

Rubiaceae

Galium asperrimum A. Gray. H; W.
Galium microphyllum A. Gray. H; SW.
Houstonia fasciculata A. Gray. N; SW.
Houstonia humifusa A. Gray. Th; SW.
Houstonia polypremoides A. Gray. Ch; SW.
Houstonia rubra Cav. H; SW.
Houstonia wrightii A. Gray. H; SW.

Caprifoliaceae

Lonicera albiflora Torr. & Gray var. *dumosa* (A. Gray) Rehd. (*L. dumosa* A. Gray.) N; W.
Symphoricarpos rotundifolius A. Gray. N; W.

Cucurbitaceae

Apodanthera undulata A. Gray. H; SW.
Cucurbita foetidissima H. B. K. H; W.
Ibervillea tenuisecta (A. Gray) Small. H; SW.

Lobeliaceae

Lobelia cardinalis L. subsp. *graminea* (Lam.) McVaugh. (*L. splendens* auth.) H; NA.

Compositae

Actinea odorata (DC.) Kuntze. Th; W.
Actinea scaposa (DC.) Kuntze var. *linearis* (Nutt.) Robinson. H; W.
Actinea vaseyi (A. Gray) Kuntze. H; MN.
Aphanostephus ramosissimus DC. Th; SW.
Aplopappus gracilis (Nutt.) A. Gray. Th; W.
Aplopappus spinulosus (Pursh) DC. var. *scabrellus* (Greene) Blake. H; W.
Artemisia albula Wooton. H; SW.
Artemisia filifolia Torr. N; W.
Artemisia carruthii Wood var. *wrightii* (A. Gray) Blake. H; W.
Aster ericoides L. H; NA.
Aster leucelene Blake. H; W.
Aster linearis (Greene) Cory. (*Machaeranthera linearis* Greene.) H; SW.
Aster tanacetifolius H. B. K. Th; W.
Baccharis emoryi A. Gray. N; W.
Baccharis glutinosa Pers. M; Tr.
Baccharis ramulosa (DC.) A. Gray. N; SW.
Baccharis wrightii A. Gray. Ch; W.
Bahia absinthifolia Benth. var. *dealbata* (A. Gray) A. Gray. (*B. dealbata* A. Gray.) H; SW.
Baileya multiradiata Harv. & Gray. H; SW.
Berlandiera lyrata Benth. H; SW.
Brickellia californica (Torr. & Gray) A. Gray. (*Coleosanthus californicus* (Torr. & Gray) Kuntze.) N; W.
Brickellia fendleri A. Gray. (*Coleosanthus fendleri* (A. Gray) Greene.) N; SW.
Brickellia laciniata A. Gray. (*Coleosanthus laciniatus* (A. Gray) Kuntze.) N; SW.
Calycoseris wrightii A. Gray. Th; SW.
Chrysactinia mexicana A. Gray. Ch; SW.
Chrysopsis fulcrata Greene. H; W.
Chrysothamnus pulchellus (A. Gray) Greene. N; W.
Chrysothamnus pulchellus var. *baileyi* (Woot. & Standl.) Blake. (*C. baileyi* Woot. & Standl.)
Chrysothamnus pulchellus var. *elatior* (Standl.) Kittell. (*C. elatior* Standl.) Wooton, Oct. 12, 1912 (U. S. Natl. Herb.), collected at Jornada Experimental Range, is the type specimen. Recorded by Wooton and Standley (1915, p. 663) and by Tidestrom and Kittell (1941, p. 394). Apparently known only from the type collection.
Chrysothamnus viscidiflorus (Hook.) Nutt. N; W.
Cirsium ochrocentrum A. Gray. H; W.
Conyza coulteri A. Gray. Th; W.
Dicranocarpus parviflorus A. Gray. Th; SW.
Dyssodia acerosa DC. Ch; SW.
Dyssodia papposa (Vent.) Hitchc. Th; W.
Erigeron bellidiastrum Nutt. Th; W.
Erigeron canadensis L. Th; NA.
Flourensia cernua DC. N; SW.
Franseria acanthicarpa (Hook.) Coville. (*Gaertneria acanthicarpa* (Hook.) Britton.) Th; W.

Gaillardia pinnatifida Torr. Th; W.
Gaillardia pulchella Foug. Th; W.
Gnaphalium chilense Spreng. Th; W.
Gutierrezia lucida Greene. Ch; W.
Gutierrezia sarothrae (Pursh) Britton & Rusby. Ch; W.
Gutierrezia sphaerocephala A. Gray. Th; SW.
Helianthus canus (Britton) Woot. & Standl. Th; SW.
Helianthus ciliaris DC. H; SW.
Helianthus petiolaris Nutt. Th. W.
Hymenopappus robustus Greene. H; SW.
Hymenothrix wislizeni A. Gray. Th; SW. College Ranch.
Iva dealbata A. Gray. Th; SW.
Kuhnia rosmarinifolia Vent. H; SW.
Malacothrix fendleri A. Gray. Th; SW.
Melampodium leucanthum Torr. & Gray. H; W.
Othake sphacelatum (Nutt.) Rydb. (*Polypteris sphacelata* (Nutt.) Trel.) Th; W.
Parthenium incanum H. B. K. N; SW.
Parthenium lyratum A. Gray. H; SW.
Pectis angustifolia Torr. Th; W.
Pectis filipes Harv. & Gray. Th; SW. College Ranch.
Pectis papposa Harv. & Gray. Th; SW. College Ranch.
Pectis prostrata Cav. Th; Tr.
Perezia nana A. Gray. H; SW.
Perezia wrightii A. Gray. H; SW.
Perityle coronopifolia A. Gray. H; SW.
Pinaropappus parvus Blake. H; SW.
Porophyllum scoparium A. Gray. Ch; SW.
Psilostrophe tagetinae (Nutt.) Greene. H; W.
Pyrrhopappus multicaulis DC. (*Sitilias multicaulis* (DC) Greene.) H; SW.
Sanvitalia aberti A. Gray. Th; SW.
Sartwellia mexicana A. Gray. Th; SW.
Selloa glutinosa Spreng. Ch; SW.
Senecio longilobus Benth. Ch; W.
Senecio riddellii Torr. & Gray. H; W.
Sonchus asper (L.) Hill. Th; I.
Stephanomeria pauciflora (Torr.) A. Nels. (*Ptiloria pauciflora* (Torr.) Raf.) H; W.
Tetradymia filifolia Greene. N; NM.
Thelesperma longipes A. Gray. H; SW.
Thelesperma megapotamicum (Spreng.) Kuntze. (*T. gracile* (Torr.) A. Gray.) H; W.
Townsendia exscapa (Richards.) Porter. H; W.
Townsendia strigosa Nutt. H; W.
Trixis californica Kellogg. N; SW. College Ranch.
Verbesina encelioides (Cav.) Benth. & Hook. var. *exauriculata* Robins. & Greenm. Th; W.
Viguiera dentata (Cav.) Spreng. H; SW.
Viguiera longifolia (Robins. & Greenm.) Blake. T; SW.
Viguiera stenoloba Blake. N; SW.
Xanthium saccharatum Wallr. Th; NA.
Zexmenia brevifolia A. Gray. N; SW.
Zinnia grandiflora Nutt. Ch; W.
Zinnia pumila A. Gray. Ch; SW.

Summary

Jornada Experimental Range is an area of 302 square miles in Dona Ana County, southern New Mexico. Most of it is in the plain of Jornada del Muerto, 4,000 to 4,600 feet above sea level, with semidesert (Lower Sororan) grass and shrub vegetation; part is on the San Andres Mountains and foothills

that rise into the woodland (Upper Sonoran) zone to a maximum elevation of 8,000 feet.

A collection of specimens of 528 species of ferns and seed plants representing 301 genera and 82 families, together with a few lower plants, was made here by the Forest Service from 1915 to 1939. A list of the species is included. The families having greatest representation, with the numbers of species in each, are: Compositae, 87; Gramineae, 80; Leguminosae, 33; Cactaceae, 16; Cruciferae, 15; and Euphorbiaceae, 15. A few are State records and extensions of known range.

The flora is western and more distinctly southwestern in distribution. More than two-fifths of the species occur from western Texas to southern Arizona and northern Mexico and more than two-fifths additional range widely in the western half of the United States.

When the species were classified on the basis of Raunkiaer's life forms, hemicryptophytes and therophytes showed the greatest excesses in percentage over Raunkiaer's normal spectrum, and the percentage of phanerophytes was far below that standard. Approximately half the species are perennial herbs, one-fourth annual herbs, and one-fourth woody plants, mainly semidesert shrubs. Only 13 species here have the size and habit of trees. Most of the plants have unusually small leaves.

A statistical analysis of the vegetation is presented, based upon data compiled from range surveys and listing the species that make up nearly all the vegetation. Only about one-third of the vegetation has high value and the rest is of low forage value or none. The native vegetation is valuable chiefly as forage for livestock, which in this locality are mainly cattle grazed yearlong.

REFERENCES

BAILEY, VERNON. 1913—Life zones and crop zones of New Mexico. U. S. Biol. Surv., North Amer. Fauna **35**:100 p., illus.

BLAKE, S. F. AND ALICE C. ATWOOD. 1942—Geographical guide to floras of the world. An annotated list with special reference to useful plants and common names. Part I. U. S. Dept. Agr. Misc. Pub. **401**: 336 p.

CAMPBELL, R. S. 1929a—Vegetative succession in the prosopis and dunes of southern New Mexico. Ecology **10**:392-398, illus.

———1929b—A case of phyllody in *Yucca elata*. Bot. Gaz. **88**:109-110, illus.

———1931—Plant succession and grazing capacity on clay soils in southern New Mexico. Jour. Agr. Research **34**:1027-1052, illus.

——— AND E. H. BOMBERGER. 1934—The occurrence of *Gutierrezia sarothrae* on *Bouteloua eriopoda* ranges in southern New Mexico. Ecology **15**: 49-61, illus.

——— AND IMOGENE FOLTZ CAMPBELL. 1938—Vegetation on gypsum soils of the Jornada plain, New Mexico. Ecology **19**:572-577, illus.

——— AND EDWARD C. CRAFTS. 1939—How to keep and increase black grama on southwestern ranges. U. S. Dept. Agr. Leaflet **180**: 8 p., illus.

——— AND J. G. KELLER. 1932—Growth and reproduction of *Yucca elata*. Ecology **13**:364-374, illus.

——— AND J. G. KELLER. 1933—Partial phyllody in *Yucca elata*. Bot. Gaz. **94**: 619-620, illus.

CANFIELD, R. H. 1934—Stem structure of grasses on the Jornada Experimental Range. Bot. Gaz. **95**:636-648, illus.

———1939—The effect of intensity and frequency of clipping on density and yield of black grama and tobosa grass. U. S. Dept. Agr. Tech. Bul. **681**: 32 p., illus.

CORY, V. L. AND H. B. PARKS. 1937 [1938]—Catalogue of the flora of the State of Texas. Tex. Agr. Exp. Sta. Bul. **550**:130 p., illus.

DAYTON, W. A. 1931—Important western browse plants. U. S. Dept. Agr. Misc. Publ. **101**:214 p., illus.

———1939—*Selenia dissecta* in New Mexico. Rhodora **41**:189-190.

——— AND OTHERS. 1937—Range plant handbook. Forest Service, U. S. Dept. Agr.

DUNHAM, KINGSLEY CHARLES. 1935—The geology of the Organ Mountains with an account of the geology and mineral resources of Dona Ana County, New Mexico. N. Mex. School of Mines Bul. **11**:272 p., illus.

EMERSON, FRED W. 1935—An ecological reconnaissance in the White Sands, New Mexico. Ecology **16**:226-233, illus.

FOREST SERVICE, UNITED STATES DEPARTMENT OF AGRICULTURE. 1914—Notes on national forest range plants. Part 1. Grasses. U. S. Forest Service, Office of Grazing Studies, 224 p.

———1925—Instructions for national forest range plant work. U. S. Forest Service Circ., 4 p.

———1932—Instructions for grazing reconnaissance on national forests. 40 p., mimeographed.

FORSLING, C. L. 1919—Chopped soapweed as emergency feed for cattle on southwestern ranges. U. S. Dept. Agr. Bul. **745**:20 p., illus.

FOSBERG, F. RAYMOND. 1931—The cacti of the Pyramid Peak region, Dona Ana County, New Mexico. South. Calif. Acad. Sci. Bul. **30**:67-73, illus.

———1940—The aestival flora of the Mesilla Valley region, New Mexico. Amer. Midland Nat. **23**:573-593, illus.

——— AND JOSEPH EWAN. 1935—Notes on southwestern plants. South. Calif. Acad. Sci. Bul. **34**:177-183.

HITCHCOCK, A. S. 1935—Manual of the grasses of the United States. U. S. Dept. Agr. Misc. Publ. **200**:1040 p., illus.

JARDINE, JAMES T., AND CLARENCE L. FORSLING. 1922—Range and cattle management during drought. U. S. Dept. Agr. Bul. **1031**: 83 p., illus.

——— AND LEON C. HURTT. 1917—Increased cattle production on southwestern ranges. U. S. Dept. Agr. Bul. **588**: 32 p., illus.

JOHNSTON, IVAN M. 1940—The floristic significance of shrubs common to North and South American deserts. Arnold Arboretum Jour. **21**:356-363. 1940.

KEYES, CHARLES ROLLIN. 1905—Geology and underground water conditions of the Jornada del Muerto, New Mexico. U. S. Geol. Surv. Water—Supply and Irrig. Paper **123**: 42 p., illus.

LESDAIN, BOULY DE. 1932—Lichens de l'État de New-Mexico (U. S. A.) recueillis par le Frère G. Arsène Bruard. Ann. Crypt. Exot. **5**:89-139.

LITTLE, ELBERT L., JR. 1937a—A study of poisonous Drymaria on southern New Mexico ranges. Ecology **18**:416-426, illus.

———1937b—Bryophytes of the Jornada Experimental Range, New Mexico. Bryologist **40**:81-83.

——— AND JOHN G. KELLER. 1937—Amphibians and reptiles of the Jornada Experimental Range, New Mexico. Copeia **1937**:216-222.

NELSON, E. W. 1934—The influence of precipitation and grazing upon black grama grass range. U. S. Dept. Agr. Tech. Bul. **409**: 32 p., illus.

RAUNKIAER, C. 1934—The life forms of plants and statistical plant geography. 632 p., illus.

RYDBERG, P. A. 1922—Flora of the Rocky Mountains and adjacent plains. Ed. 2, 1143 p.

STANDLEY, PAUL C. 1910a—The type localities of plants first described from New Mexico. U. S. Natl. Mus., Contrib. U. S. Natl. Herbarium **13**:143-227, illus.

———1910b—A bibliography of New Mexican botany. U. S. Natl. Mus., Contrib. U. S. Natl. Herbarium **13**:229-246.

———1913—Descriptions of new plants preliminary to a report upon the flora of New Mexico. U. S. Natl. Mus., Contrib. U. S. Natl. Herbarium **16**:109-196.

———1916a—Comparative notes on the floras of New Mexico and Argentina. Wash. Acad. Sci. Jour. **6**:236-244.

———1916b—Fungi of New Mexico. Mycologia **8**:142-177.

———1920-26—Trees and shrubs of Mexico. U. S. Natl. Mus., Contrib. U. S. Natl. Herbarium **23**:1721 p.

TIDESTROM, IVAR. 1925—Flora of Utah and Nevada. U. S. Natl. Mus., Contrib. U. S. Natl. Herbarium **25**: 665 p., illus.

——— AND SISTER TERESITA KITTELL. 1941—A flora of Arizona and New Mexico. 897 p., illus.

WALLACE, SUSAN E. 1888—The land of the pueblos. 285 p., illus. New York.

WILLIAMS, R. S. 1936—*Moenkemeyera littlei*, sp. nov. Bryologist **39**:40-41, illus.

WISLIZENUS, A. 1848—Memoir of a tour to northern Mexico, connected with Col. Doniphan's Expedition in 1846 and 1847. 30th Cong., 1st Sess., Misc. No. **26**: 141 p.

WOOTON, E. O., AND PAUL C. STANDLEY. 1915—Flora of New Mexico. U. S. Natl. Mus., Contrib. U. S. Natl. Herbarium **19**: 794 p.

FOREST SERVICE,
UNITED STATES DEPARTMENT OF AGRICULTURE,
WASHINGTON, D. C.

New Species and Transfers in Myxophyceae

Francis Drouet

Specimens listed here are to be found in herbaria designated by the following abbreviations: C, Herbarium of the University of California; D, Herbarium of F. Drouet; F, Farlow Herbarium of Harvard University; FM, Cryptogamic Herbarium, Field Museum of Natural History. Where their location has not thus been noted, it is to be understood that they are on file in Field Museum.

Entophysalis rivularis (Kütz.), comb. nov.

Hydrococcus rivularis Kütz. Linnaea **8**:380. 1833. *Oncobyrsa rivularis* Menegh. Mem. R. Accad. Torino 2. ser., **5**:96. 1848. *Hydrococcus Cesatii* Rabenh. Alg. Sachs. 65 & 66: 922. 1860. *Oncobyrsa Cesatiana* Rabenh. Fl. Eur. Alg. **2**:68. 1865.

The structure of the plants which pass in the literature under the names cited as synonyms above proves to be so very similar to that of *Entophysalis granulosa* Kütz. (*Placoma vesiculosa* Schousb.) that I find it imperative to propose this transfer.[1] I have not had the opportunity to see Kützing's original specimens of *Hydrococcus rivularis* from between Schleussingen and Sohl, Thüringen; I follow here the interpretation of the type by Edouard Bornet and by Anton Hansgirg, as indicated by the specimens which they determined.

Specimens seen: BOHEMIA: in aqueducto ligneo fontis in silva Hercynica ad Deffernik prope Eisenstein, *A. Hansgirg*, Aug. 1887 (as *Oncobyrsa rivularis*, Wittr. & Nordst. Alg. exs. 999: C, FM). ITALY: ad Fontinalem antipyreticam in rivulis all'Oropa Bugellens., Piedmont, *Cesati*, Aug. 1859 (isotype of *Hydrococcus Cesatii* and *Oncobyrsa Cesatiana*, Rabenh. Alg. Sachs. 922: C, FM; Erb. Crittogam. Ital. 456: C). FRANCE: Vosges, *ex herb. Lenormand* (D). NEW HAMPSHIRE: on hepatic, Chocorua, *W. G. Farlow*, 1906 (F); on *Hypnum Lescurii*, Bowls and Pitchers, Shelburne, *Farlow*, Oct. 1899 (F, FM); on *Hydrothyria venosa*, Ingalls brook, Shelburne, *E. Faxon*, Sept. 1886 (D, F). MASSACHUSETTS: on Lemanea, Waverly, *W. H. Weston, jr.*, June 1923 (FM). PENNSYLVANIA: on Lemanea, Wissahickon creek, Philadelphia, 1854 (F); Derry church, Dauphin county, *F. Wolle*, Oct. 1887 (D, FM). MINNESOTA: on *Lemanea torulosa*, Lester river, Duluth, *E. Butler*, Aug. 1902 (F, FM). MISSOURI: on mosses and rocks, Gravois spring, Gravois Mills, Morgan county, *Drouet 682, 882, 1234*, Sept. 1930, May 1931, Aug. 1934 (D). ALASKA: on mosses in a brook near Iliuliuk, Unalaska island, *W. A. Setchell & A. A. Lawson 5036*, June—Aug. 1899 (C, FM).

1 It would seem especially desirable to abandon separate generic status for *E. rivularis* since a portion of the type collection of *Oncobyrsa fluviatilis* Ag. Flora 629 (1827), type species of *Oncobyrsa* Ag. *loc. cit.*, found in the Farlow Herbarium, proves to contain only Chlorophyceae; this fact has been pointed out by Kützing, Trevisan, Forti, and others. Moreover, the publication of *Hydrococcus* Kütz. Linnaea **8**: 380 (1833) was made during the same year (or if I interpret Trevisan Sagg. Monogr. Alg. Coccot. 73 [1848] correctly, at a later date than this) as *Hydrococcus* Link Handb. **3**:268 (1833).

Dermocarpa caldaria (Tild.), comb. nov.

Protococcus botryoides f. *caldarius* Tild. Bot. Gaz. **25**: 94, pl. 8, f. 18. 1898. *Pleurocapsa caldaria* Setch. Phyc. Bor.-Amer. **18**: 851. 1901.

This species, found only in hot springs, is here considered as an unattached form related morphologically to *Dermocarpa Schousboei* (Thur.) Born. and *D. Hollenbergii* Dr. J. J. Copeland in Ann. New York Acad. Sci. **36**:72, f. 33 (1936) proposed its segregation into a separate genus[2] of the Dermocarpaceae, but without a Latin diagnosis for the new name. The distribution of *D. caldaria* as now known to me is indicated by the following specimens in the Cryptogamic Herbarium of Field Museum.

WYOMING: on bottom of spring, temperature 38° C., Frying Pan basin, Yellowstone national park, *J. E. Tilden*, July 1896 (isotype in Tild. Amer. Alg. 283). CALIFORNIA: warm stream at sulfur works, Mt. Lassen, *L. Bonar 7836*, July 1934; on steaming rocks above Devils Kitchen, The Geysers, Sonoma county, *W. A. Setchell & L. E. Hunt*, June 1900 (as *Pleurocapsa caldaria* in Phyc. Bor.-Amer. 851); in hot water basins, The Geysers, Sonoma county, *O. L. Inman*, July 1939 (as *Chlorella* sp. reported by Inman, Journ. Gen. Physiol. 23: 664. 1940); on rocks around solfataria fumaroles near the summit pinnacle, Mt. Shasta, *T. L. Johnston 14671*, Aug. 1940. GUATEMALA: in hot water, Aguas Amargas and Fuentes Georginas, slopes of Volcán de Zuníl, Dept. Quezaltenango, *P. C. Standley 83381, 83387, 83391, 86020, 86022*, Jan.—Feb. 1941.

Schizothrix Richardsii, sp. nov.

Fila longa recta subrigida, basi trunciformia, fasciculato-ramosa, in stratum extensum pannosum aerugineum vel subnigrum crescentia, supra in fasciculos erectos vel decumbentes torta, ramis longis gracilibus subrigidis lyngbyoideis; vaginis primum hyalinis papyraceis, aetate provecta roseis vel pallide rubris incrassatis et fibrosis, ambitu erosis, chlorozincico iodurato laete caerulescentibus; trichomatibus aerugineis, 4μ ad 7μ crassis, ad genicula non constrictis, ad apices attenuatis atque subcapitatis; cellulis subquadratis vel diametro 1½-plo longioribus, protoplasmate granuloso, dissepimentis conspicuis; cellula apicali conica, membrana superna rotundata incrassata.

This is one of the most conspicuous constituents of the pannose algal strata covering barren ground in Sonora. Unless the sheaths are treated with chlor-zinc-iodine, the observer is apt to misinterpret this species as a peculiar form of *Microcoleus vaginatus* Gom., under which name certain specimens listed below have been distributed from Field Museum to other herbaria. *Schizothrix Richardsii*, named for Mr. Donald Richards of Field Museum, is a member of Gomont's section Chromosiphon, related morphologically to *S. thelephoroides* Gom. and *S. acuminata* (Gardn.)Dr. It differs most remarkably from these latter species in the thickened membranes of its mature apical cells.

---

2 **Pluto** J. J. Copeland, gen. nov.

Plantae unicellulares sphaericae natantes, membrana levi; cellulis grandibus in gonidiis quaternis dividentibus; reproductione haud vegetativa.

One species **P. caldarius** (Tild.) Copeland, comb. nov. *Protococcus botryoides* f. *caldarius* Tild. Bot. Gaz. **25**: 94. 1898.

Specimens seen: SONORA: Villa de Seris, *Drouet, Richards, & L. D. Alvarado 2813, 2817, 2820, 2859*, Nov. 1939; near the airport, Hermosillo, *Drouet & Richards 2875*, Nov. 1939; 7 miles north of Bahia Kino, *Drouet & Richards 2892, 2893*, (TYPE in the Cryptogamic Herbarium, Field Museum), *2894*, Nov. 1939; dunes and sandhills near Bahia Kino, *Drouet & Richards 2895, 2904, 2906*, Nov. 1939; northwestern edge of Guaymas, *Drouet & Richards 3316*, Dec. 1939; Aurora, south of Baviácora, *Drouet & Richards 2949*, Nov. 1939.

Schizothrix Taylorii, sp. nov.

Fila inter alias algas gregaria vel in stratum nigrum cartilagineum coalita, subrecta subrigida subparalleliter crescentia, basi ramosa, vaginis primum tenuibus hyalinis, aetate provecta incrassatis caeruleis et intus nigro-chalybeis, lamellosis, ambitu levibus vel erosis, chlorozincico iodurato caerulescentibus; trichomatibus pallide aerugineis, 4μ ad 7μ crassis, ad genicula constrictis, frequenter torulosis, ad apices attenuatis et acuminatis; cellulis quadratis vel diametro brevioribus vel longioribus, protoplasmate inconspicua granuloso, dissepimentis non granulatis; cellula apicali primum brevi-conica, aetate provecta longe et acutissime conica.

With other algae in crusts on barren ground, in crevices of rocks, and in ephemeral rain-pools. This species, named in honor of Professor William Randolph Taylor of the University of Michigan, is to be placed among the blue-sheathed species of Gomont's section Chromosiphon near *S. chalybea* Gom. It differs markedly from the latter species in the nature of its sheaths, the size of its trichomes, and the configuration of its apical cells. In the type specimen the plants are growing among other algae; almost pure growths are to be seen in the Florida specimens cited below, but in these the blue color is well developed in the sheaths of very few filaments.

FLORIDA: Marco island, Collier county, *P. C. Standley 73399, 73401, 73410*, Mar. 1940; with *S. longiarticulata* Gardn., south shore of Big Pine key, Monroe county, *M. A. Cornman*, Mar. 1943. SONORAS Cerro de la Campaña, Hermosillo, *Drouet, Richards, & Alvarado 2787*, southwest of Villa de Seris, *Drouet, Richards, & Alvarado 2819* (TYPE in the Cryptogamic Herbarium, Field Museum), *2851*, canyon 11 miles northeast of Baviácora, *Drouet, Richards, & Lockhart 2982*, canyon west of Rio de Sonora, Baviácora, *Drouet, Richards, & Lockhart 2951*, Nov. 1939. GUATEMALA: vicinity of Zacapa, *Standley 73634*, Oct. 1940. VENEZUELA: high rain-pool, shore of Cubagua island, *Taylor 475b*, Apr. 1939.

Oscillatoria Maldonadoana, sp. nov.

Trichomata aeruginea vel pallide lutescenti-aeruginea, inter alias algas aquaticas crescentia, longa fragilia, recta vel subflexuosa, 2μ ad 4μ crassa, ad genicula non aut vix constricta, ad apices recta longe et sensim attenuata atque quasi-truncata; cellulis quadratis vel diametro plus minusve brevioribus vel longioribus, protoplasmate aerugineo non granuloso, dissepimentis haud granulatis; cellula apicali rotundata vel quasi-truncato-conica.

With *Ctenocladus circinnatus* Borzi and other algae in shallow inland salt water. This species belongs in Gomant's section Attenuatae near *O. amoena* Gom. and *O. granulata* Gardn.; from both of these latter it differs in size of

trichome, in configuration of the apices, and in the general appearance of the protoplasm and cross-walls. It is named in honor of Professor Angel Maldonado of Lima, Peru.

One collection, PERU: Laguna Boza, dist. Huaral, prov. Chancai, dept. Lima, *Maldonado 301b*, Jan. 1943 (TYPE in the Cryptogamic Herbarium, Field Museum).

Oscillatoria Gardneriana, sp. nov.

Stratum tenue fragile laete aerugineum, trichomatibus longis rectis fragilibus, 4μ ad 6μ crassis, ad genicula non constrictis, ad apices brevi-attenuatis acutissimis nonnumquam uncinatis; articulis brevibus, diametro 2-4-plo brevioribus, protoplasmate laete aerugineo, dissepimentis pellucidis inconspicua granulatis; cellula apicali longe conica mucronata.

Growing on mud in brackish water. This species, a member of Gomont's section Attenuatae, resembles *O. brevis* Gom. closely except in the mucronate apices of its trichomes. It is named in memory of the late Professor Nathaniel Lyon Gardner of the University of California.

One collection, CALIFORNIA: on mud in a brackish roadside ditch east of Martinez, Contra Costa county, *Gardner 7061*, Oct. 1932 (TYPE in the Cryptogamic Herbarium, Field Museum; isotype in the Herbarium of the University of California).

FIELD MUSEUM OF NATURAL HISTORY,
CHICAGO, ILL.

Revision of the Giant West Coast Land Slugs of the Genus Ariolimax Moerch (Pulmonata: Arionidae)

Albert R. Mead

The giant West Coast land slugs have a complex genital physiology (Heath, 1916), the details of which are unknown, except that they frequently gnaw off the penis at the close of copulation. The first step in a study of this behavior undertaken by the author was to examine critically a great number of specimens not only to familiarize himself with the genital morphology of the several species in the hypertrophied, atrophied, and immature states, but to attempt to find a structural explanation for this unique practice. Examination of large series of live specimens afforded great advantages which earlier workers unfortunately had not enjoyed; consequently the literature contains not only serious errors regarding the taxonomic status of the group, but also many morphological misinterpretations based on examinations of very limited and often poorly preserved material. For this reason, it was thought advisable to publish first a revision of the taxonomy of this genus with adequate information on its speciation, phylogeny, and distribution. In this paper the morphological aspects are limited to those external and internal structures, which are or have been considered of taxonomic importance. Other structures, including especially the apical genital structures, will be treated in a later paper dealing with the biology and genital physiology of the genus.

Many factors are responsible for this confusion in the literature. They are here listed in the order of decreasing importance: artifacts of preservation, lack of live material, insufficient material, almost complete absence of external diagnostic characters, dimorphism in *A. columbianus*, apophallation (loss of penis), anomalies of internal structures, and unique specimens.

The use of the following technique in the examination of a great number of live specimens taken from many localities and at different seasons of the year removed many difficulties. After recording the weight of the specimen, it is put in a cool saturated solution of chloretone which is prepared by dissolving the crystals in hot boiled tap water. It is necessary to boil the water to remove all the air. If tissues are to be saved for histological study, the specimen is examined within twenty minutes to an hour later; otherwise from one to six hours is satisfactory though the integument continues to take up a great deal of water. There is less contraction and less slime exuded upon cutting if the specimen remains in the chloretone solution for the longer period of time. Rolling the specimen on dry paper towels removes almost all of the slime. It is then anchored in a wax bottom tray containing 7.5% normal saline by putting a pin through the dorsal integument as the specimen rests on its right side. With one clip of the scissors, the caudal slime gland is cut away. This affords an easy entrance of the scissors into the body cavity

for the lateral incision which is made close to the striate portion of the sole and extended to the head. The contracting body wall is then pulled out and pinned. The slime and blood are drawn off with a pipette and more saline is added if necessary. The thin mesentery surrounding the viscera is removed and the rectum and aorta are cut. Then the genital structures are freed from the folds of the viscera. The alimentary canal and brain mass are removed after cutting loose the connecting nerves and odontophore. As the tentacular retractors are cut, they contract out of the way leaving the genital structures completely unobstructed. The specimen is merely anethetized and it is indeed a thrill to see the genital structures writhing, extending, and contracting in serpentine fashion and to observe what goes on inside the living animal.

Heretofore no attempt has ever been made in the literature to present adequate synonymies in this genus, principally because the species and their distribution were too little understood. For this reason, the synonymy of each species has been compiled as far as possible, though some references may have been missed. Since all important works dealing with the genus are discussed in the treatment of the species, it was unnecessary to prepare a synonymy for the genus.

Every effort has been made to locate the types of *columbianus* and *californicus* but with no success. Binney (1885:484) lists a type of *californicus* as being in his collection. Gratacap (1901) similarly lists this species in his catalogue of the Binney and Bland collection and states, "It also includes the specimens used by Amos Binney and Augustus A. Gould in the preparation of their 'Terrestrial Air-Breathing Mollusks of the United States'." This statement suggested that the *columbianus* types might also be in this collection. Unfortunately neither was found there and the fate of these types must be determined in the future.

The writer is indebted to many for help in the preparation of this work. Especial thanks are extended to Dr. W. H. Lange of the University of California, who provided many specimens and generously contributed all of the locality records from his own manuscript; and to Professor T. I. Storer of the same institution, whose council and encouragement in the early phases of this work will always be gratefully remembered. Mr. George Kanakoff of the Los Angeles Museum unstintingly supplied information and material which he gathered on the Channel Islands Survey conducted by the Los Angeles Museum. Sincere thanks are due him for granting the writer permission to publish the new and very significant Santa Rosa Island record. The writer wishes to express his indebtedness to Dr. H. A. Pilsbry of the Academy of Natural Sciences of Philadelphia and Professor H. B. Baker of the University of Pennsylvania for their counsel and advice on many of the finer aspects of this work; to Dr. Joshua Baily of San Diego, Professor Paul Bartsch of the Smithsonian Institution, Professor T. D. A. Cockerell of the University of Colorado, Dr. W. O. Gregg of Los Angeles, Dr. G. Dallas Hanna of the California Academy of Sciences, Professor Harold Heath of the Hopkins Marine Station, and Mr. R. J. Waste of Chico State College who have contributed no small part by offering valuable information and suggestions; to Professor B. P. Young and Dr. W. T. M. Forbes of Cornell University who have given freely of their time in examining the manuscript; to Professor G. D. Harris of Ithaca, New York, who so kindly put his extensive library at the writer's disposal; and to Mr. A. L. Smith also of Cornell who made the photographs. It is indeed unfortunate that limited space forbids the listing here of the many others who have contributed specimens, authentic locality records, and helpful suggestions for which the writer is sincerely grateful.

Genus ARIOLIMAX Mörch

Mörch (1860) early recognized that Gould's *Limax columbianus* was closely related to *Arion* and gave it the name *Ariolimax*. Mörch's work apparently remained in relative obscurity for the name *Limax* was used in later references (Binney, 1863; Carpenter, 1864) to this species. Even as late as 1868, Tryon still used this name. It was not until 1865 that Mörch's work was brought to the attention of American conchologists by Binney who presented at the same time his own observations on the external anatomy, radula, etc. Carpenter (1864), however, in a footnote quotation from a manuscript of Binney, indicates that Binney had apparently independently considered this species an arionid. The footnote states, "Has a pore. Why not Arion?" In this work of Carpenter, there are given data from Binney's manuscript which include a list of specimens and the first Oregon and California records for this genus. The list appears again in 1869 when Binney published this manuscript. These specimens unfortunately were burned in the Chicago fire and he was forced to obtain new material in order to complete with Bland his studies on the external anatomy (1874). That same year, he published the first study of the internal anatomy and, even though he was led by Leidy's terminology to misinterpret some of the structures, he nevertheless opened up a new field in the interpretation of specific differences in this genus. As will be shown below, his contemporaries were slow in accepting this and thereby continued to clutter up the literature with misidentifications and synonyms based solely on highly variable external characters.

Simroth's careful work (1891a, b) revealed for the first time the true nature of many of the internal structures. The work of Pilsbry and Vanatta (1896) corrected nearly all of the remaining misconceptions and has remained to date the most comprehensive work on this genus. At that time, they described the new genus *Aphallarion* which is shown below, in the remarks on *columbianus,* to be synonymous with *Ariolimax*. With their work treating in adequate detail the characters of the genus, there will be little need here to discuss these again except to point out certain corrections, confirmations, or new conclusions, reached as a result of an intensive study of over 700 specimens of the three species and two subspecies in this genus.

External Characters.—Color is almost entirely unreliable in distinguishing species, especially with preserved specimens. It is very variable in *columbianus* but it apparently never attains the light yellow color of the others which are less variable. Individuals will change in color surprisingly over a period of time with alterations of food, moisture, and/or light. Color will also change with age. Maculation is found only in *columbianus* and is discussed under that species below.

Statements of the *dimensions* of preserved specimens are practically worthless except as to indicate whether the slug is large or small. Even with live specimens, measurements are of only slight significance as again, nutrition, seasonal atrophy and hypertrophy, and many other factors may result in great discrepancies in size. For example, a six month old specimen of *califor-*

nicus was given near optimum conditions of food and moisture, and a year later it weighed 37 grams, over twice the normal weight for this age, but was still sexually immature! The live weight is, of course, the most dependable measure of size. Averages of the length of the fully extended foot and the weight of a great number of larger individuals in a population will give figures for each species and subspecies which seem to be somewhat significant.

The relative number of *striae* and the transverse or oblique nature of the *cross striae* were thought to be diagnostic by Cooper (1872 etc.), but he proved by his own confusion that neither of these can be so considered.

The *keel* or *carina* cannot possibly be used in distinguishing between species. In the same slug it may be very acute, as when fully extended or when subjected to extreme cold or dryness, whereas on the other hand if it is subjected to slightly higher temperatures with a concomitant increase in humidity, or if the slug is near death, the keel will become scarcely perceptible. Obviously, improper preservation will produce an abnormal keel.

There has been frequent mention in the literature of the truncate nature of the *mantle;* this is another artifact of preservation as the margin in live specimens of all species is evenly oblong. Likewise, there is no tangible difference in the length of the mantle or its free anterior lip as it is highly contractile and frequently greatly altered with preservation. This latter accounts for the apparent granular nature of the mantle which doubtlessly persuaded Binney *et al.* to place *columbianus* in *Amalia.*

The tripartite nature of the foot or *sole,* in respect to color, is not only quite variable in nearly any population, but it is usually altered with preservation and therefore is of little use in identification. The vertical surface of the foot margin is always adorned with alternating darker and lighter vertical lines. These may be generally lighter and approaching the body color or they may be black and in strong contrast. These often fade in preservation and this is the reason that Pilsbry and Vanatta (1896) stated that the "foot margin" of *columbianus* was "without dark vertical lines" in contrast to *californicus.* The foot is normally proportionately wider in the caudal region in this genus.

One of the most important generic characters is the *caudal pore* which always contains a groove-bordered plug of mucous tissue though this latter may be deeply withdrawn in specimens put in too strong a preserve. Its function in copulation will be explained in a later paper.

Internal Characters.—With new members added to the genus, a careful study of the *jaw* was made to see if there were specific differences. The only correlation found was a generally lower number of ridges in immature specimens, as might be expected. The ridges varied indiscriminately from 11 to 19 in the specimens examined.

A similar study of the *radula* proved equally unfruitful as they all possessed the same "arionid type" with often greater variation within a species

than between different species. The formulae varied indiscriminately from 60-1-60 x 129 to 67-1-67 x 158 and 70-1-70 x 152. Occasional differences were found in the median teeth but these proved inconsistent. Infrequently the same lateral tooth in every transverse row would be found to be unlike the rest (e.g., a nipple-shaped mesocone) but this was presumably caused by some abnormality in the tissue generating this longitudinal row.

Early writers made a distinction in the *shell* plates of *californicus* and *columbianus*. We now know there is absolutely no specific difference. Instead, this structure is a better index of nutrition and calcium metabolism. Confirmation has been made of Cooper's early statement (1872) that egg laying causes a complete absorption of the shell. It might be added, however, that there is usually only a partial absorption and that the shell is never "entirely wanting," for there always remains a thin, flat, clear, flexible, proteinaceous "replica" of the shell which provides the foundation for subsequent calcium deposition. It is of interest to note that young slugs raised almost exclusively on milk have an extremely thick and sometimes almost amorphous shell. Further studies are being carried on along this line.

The *genital atrium* exists in all species but it is very shallow.

The *male structures* concerned in copulation are treated in detail below in the descriptions of the species and the discussion of the phylogeny.

There still remains much confusion in the literature regarding the distinctness of the *vagina* (which Simroth, 1891b, calls the "Atrium") and the *free oviduct*. The definitions of Pilsbry and Vanatta (1898) are perfectly clear, but since they were put in a footnote, they perhaps have escaped adequate attention. To insure no misunderstanding in the use of terms, it seems well to redefine them. The vagina should be defined as that basal part of the female conduit which is between the spermatheca and the atrium and which normally receives the penis as it passes to the spermatheca during copulation. The free oviduct, on the other hand, is that part of the female conduit which is between the spermatheca and the point of departure of the vas deferens from the ovisperm duct. The spermatheca thus marks the division between these two structures. The vagina is concerned mainly in copulation as well as in the deposition of eggs, whereas the free oviduct is concerned only with the latter.

In the walls of the vagina there is contained a muscle mass which heretofore has been relatively ignored or misinterpreted. It probably assists in expelling the eggs during oviposition. Since, as explained below, it also plays an important part in copulation and apophallation (loss of penis), and is of taxonomic importance and therefore will be frequently referred to, it seems advisable to give it the name *intrinsic muscle* of the vagina. This is further discussed under *californicus* in which it attains its greatest development.

A completely distinct muscular entity is the so-called "retractor muscle" of the vagina which in this genus is, because of its extent, apparently homolo-

gous to the combined "retractors" of the spermatheca and vagina and/or free oviduct of other genera in the family Arionidae. This name "retractor" has been given it apparently because in the more advanced, aphallate genera (*viz. Arion* and *Geomalacus*) the free oviduct is said to evert after the manner of a penis during copulation and is then withdrawn by the action of this muscle. It should be understood that this retractor function has come about as a purely secondary adaptation in these genera. In the lower, phallate genera, on the other hand (*Ariolimax, Hesperarion,* etc.), this muscle (or muscles) functions essentially as a retentor, keeping in place the vagina and/or spermatheca during copulation by offsetting the forceful withdrawal movements of the greatly distended penis. The term here is obviously wholly incorrect in its inference. For example, this muscle in *Hesperarion* is split similarly to that of *Arion* with one part passing to the free oviduct and one to the very elongate spermatheca, yet it very evidently does not function as a "retractor" of these structures. Since retention is the primitive function of the muscle, it might more correctly be termed the retentor muscle of the vagina, free oviduct, and/or spermatheca though this name would obviously be confused with the so-called "retensor" muscle discussed below. To avoid further confusion and the perpetuation of an inappropriate term, the term *extrinsic muscle* of the vagina has been used in this paper. As will be explained below under *columbianus,* the so-called *"Aphallarion buttoni"* does not evert the vagina as Pilsbry and Vanatta (1896) suggest.

There is a muscle, peculiar to this genus, which passes normally from its origin, on the posterior rim of the diaphragm, diagonally to the left side dorsal to the genitalia and ventral to the diaphragm. It inserts on the body wall either near the genital atrium, dorso-caudal to it between the tentacles, or in between these two points. Simroth (1891a, b) was uncertain as to the function of this muscle but offered the suggestion that it perhaps acted as a "retensor" offsetting an excessive forward increase in blood pressure on the genitalia and neighboring integument during copulation. This explanation does not seem wholly tenable and yet observations on the activities of these slugs so far have suggested nothing different. Pilsbry and Vanatta (1898) believe that it is a *retractor pedis* and suggest that it may aid in withdrawing the head beneath the mantle, but experiments with live slugs indicate no such function. Its absence in the higher slugs in this family suggests that it is "on its way out" and this consequently may be merely a carry-over from testate ancestors, with no especial function. Pilsbry adopted the term "retensor" and has used it frequently, but Babor (1900) makes the valid suggestion that it more corectly should be called *retentor.* It is interesting to note that this muscle was cleft in Simroth's specimen. The writer has found it similarly abnormal in a number of cases. If it is split, one part may pass dorsal and one ventral to the vagina either anatomosing again to make a single insertion or inserting separately. It may be split or almost duplex and yet perfectly normal in location or it may be single and pass between the vagina and the penis along with the right tentacular retractor.

Genotype.—Limax columbianus Gould (monotypic).

ARIOLIMAX COLUMBIANUS (Gould)

(Figs. 5, 8, 14, 20-22)

Limax Columbianus Gould, 1851:43, pl. 66, fig. 1.—Gould, 1852:[3], pl. 1, fig. 1, 1a-1c.—Grateloup, 1855:14.—Carpenter, 1857:210, 213, 312.—Binney, 1858:21.—Binney, 1859:6.—Binney, 1860:[1].—Cooper, 1860:377.

Limax (Amalia) Columbianus Binney, 1863:8.—Carpenter, 1864:599, 673.—Tryon, 1868:315, 323, pl. 16, fig. 1.

Ariolimax columbianus Mörch, 1860:110.—Binney, 1865:48, pl. 6.—Cooper, [*partim*] 1867:14.—Binney & Bland, 1869:xii, 279, figs. 496-501.—Cooper, [*partim*] 1870:57.—Binney, 1873:192, 196, 200.—Bland & Binney, 1873:247.—Cooper, 1873:154.—Binney, 1874:33-38, pl. 2, figs. B-H.—Bland & Binney, 1874:297.—Binney, 1876:185.—Binney, [*partim*] 1878:18, 21, 231, pl. v, fig. E; pl. xii, fig. C; text figs. 129, 130.—Binney, 1879:344.—Cooper, 1879:288.—Binney, 1883:162.—Tryon, 1884:84, pl. 101, fig. 54.—Binney, [*partim*] 1885:19, 23, 57, 98, figs. 58-61.—Heynemann, 1885:268, 271, 315.—Tryon, 1885:246.—Binney, 1886:43.—Cooper, 1887:367, 503 (line 21), 506.—Pilsbry, 1889:199.—Binney, [*partim*] 1890:211, pl. vi, fig. G.—Cockerell, 1890:278, 279.—Simroth, 1891a:112, 114.—Taylor, 1891:92.—Cockerell 1893:192.—Cooper, 1894.—Pilsbry & Vanatta, 1896:343, pl. xii, fig. 2; pl. xiii, figs. 1, 2; pl. xiv, figs. 7-10.—Cockerell, 1897:77.—Pilsbry, 1898:139.—Pilsbry & Vanatta, 1898:235, pl. xiv, fig. 66; pl. xv, figs. 73, 74, 81.—Dall [*partim*] 1905:9, 34, 35, 47.—Heynemann, 1909:23, 25.—Hanham, 1914:87.—Orcott, 1915:54, 110.—Allen, 1916:143.—Thiele, 1931:601.—Keep & Baily, 1935:296.—Pratt, 1935:606.—Waste, [*partim*] 1937:40, pl. 1, fig. 1; pl. 3, fig. 2; pl. 4, figs. 1, 2.—Ingram, 1942:99, 101.

Ariolimax californicus‡ [*nec* Cooper 1872] Cooper, 1872:147 (Sierra Nevada ref. only).—Cooper, 1876:24.—Cooper, 1886:253.—Cooper, 1887:367 (Sierra Nevada ref. only), 370, 372, 373, 375, ?*502, ?*503 (line 4).—Cooper, 1890:70.—?*Wood & Raymond, 1891:56.—Cooper, 1894.—Cockerell, 1897:76 (bottom), 77.

Ariolimax columbianus maculatus Binney, 1890:211, pl. vi, fig. A.—†Cockerell, (forma) 1891:31, 32.—Cockerell, 1893:192.—Pilsbry, 1898:139.—Dall, 1905:48.—Heynemann, 1909:25.—Orcutt, 1915:110.—Henderson, 1927:76.—Henderson, 1929:108, 110.—Keep & Baily, 1935:296.

Ariolimax subsp. *Californicus* forma *maculatus* Cockerell, 1891:31 (foot note).—Cockerell, 1897:76, 77.

Ariolimax Columbianus forma *niger* †Cockerell, 1891:32.—Cockerell, 1893:192.—Orcutt, 1915:110.

Ariolimax Columbianus forma *typicus* †Cockerell, 1891:31.—Cockerell 1893:192.

Ariolimax c[*olumbianus*] *californicus maculatus* Cockerell, 1893:192.

Aphallarion Buttoni Pilsbry & Vanatta, 1896:348, pl. xii, figs. 3-5; pl. xiii, fig. 4; pl. xiv, figs. 11, 12.—Pilsbry, [*partim*] 1898:139.—Pilsbry & Vanatta, [*partim*] 1898:236, pl. xiv, fig. 67; pl. xv, fig. 76.—Heynemann, 1909:23.—Simroth & Hoffmann, 1928:525, fig. 171, G.—Thiele, 1931:601.—Keep & Baily, 1935:296.

Ariolimax steindachneri Babor, 1900:95.—[Pilsbry], 1900:71.—?Dall, 1905:48.—Heynemann, 1909:24, 25.—Orcutt, 1915:140.—Henderson, 1929:108, 110.

Ariolimax columbianus columbianus [*partim*] Henderson, 1929:108, 109.

[*non Ariolimax columbianus* Yates, 1890:41.]

[*non Ariolimax californicus* v. *columbianus* Simroth, 1891a:111.]

[*non Ariolimax c*[*olumbianus*] *californicus* Cockerell, 1893:192.]

---

* May have been *A. c. brachyphallus*.

‡ Name cited in error.

† Erroneously listed in index to vol. as Agriolimax.

External.—Ground color deep olivaceous green, tan-green, ochraceous, ochraceous-yellow, slate green, or intermediate shades; mantle concolorous. Black maculations varying from minute spots to large irregular blotches which may fuse, to obscure the ground color, and forming an almost entirely black upper surface. Maculations may be reduced to a single persistent central spot on the mantle or may be entirely absent. Longitudinal striae variable in number, usually considerably darker in color; cross striae transverse or oblique, prominent but usually sparse. Sole frequently much wider than back; lateral striate portion concolorous or only slightly darker; concolorous or somewhat lighter beneath with lateral thirds slightly darker than median third. Very large, robust; adults 35-40 gms. up to 72 gms.; foot length when fully extended 185-260 mm.

Genitalia.—Penis a permanently partially evaginated hollow tube; slender or very robust; sheath plicate and thin walled. Papilla thick walled and plicate or vermiculate; tapering toward the atrium to a bluntly rounded, thin walled, highly expansile apex; hollow with much connective tissue attaching to the internally contained apical vas deferens; apex may be modified into a "glans." Vas deferens adjacent to penis slightly enlarged to form a slender ejaculatory duct 2 to 3 times the diameter of basal vas deferens; this tapers imperceptibly to a more slender apical vas deferens which passes internally along the median longitudinal axis of the penis papilla connecting with the latter at its apex. Retractor muscle of the penis slender and strap-shaped; origin broad at apex of penis, surrounding apical vas deferens and obscuring evagination; insertion directly anterior or anterio-lateral to aorta. Vagina short and straight, basal portion thin walled, equally long apical portion thick walled; these two portions separated by the small, thick, and annular intrinsic muscle. Extrinsic muscle of vagina thin and long with origin from intrinsic muscle to spermatheca and basal portion of free oviduct; strands converge to insertion on central diaphragm near that of retractor muscle of the penis. Spermatheca petiolate, not broadly joined to vagina; located as far apically to the intrinsic muscle as the latter is to the atrium. Free oviduct very wide and/or long with many convolutions, or if shorter and essentially unmodified, its length equal to or greater than that of vagina and exceeding that of spermatheca petiole. Genital atrium shallow.

Types.—Unknown.

Type Locality.—"This fine American species was found on the western coast of North America at Nisqually by Lieut. Case, and at Discovery Harbor, Puget Sound, by Mr. Dyes." (Gould)

Remarks.—This is the largest and most widely spread species in the genus and the only one which exhibits maculation and great color variation. The permanently partially evaginated penis alone sets this species off as distinct from all others except *stramineus*. The differences between this species and its subspecies are discussed under the latter (*q.v.*).

The vagina has been carefully defined above and we may now more intel-

ligently interpret its condition in this species. According to Binney (1874, etc.), this species is equipped with "an extremely long, convoluted vagina." Pilsbry and Vanatta (1896) mention that it possesses "a rather long vagina." Babor (1900) believed there was no special vaginal formation (*vide post*). The vagina is well defined and not long but characteristically short; it is the free oviduct which is usually very long and thrown into several loose coils and folds, though it occasionally is found considerably shortened and uncoiled hence approaching the condition in *stramineus*. This difference in length and modification has been observed in both Washington and California specimens and its significance will be pointed out in a later paper treating the genital physiology of the genus.

Other remarks regarding the genital system in this species concern the nature and interpretation of the penis which never before has been clearly understood. These are discussed in detail below in the comparative morphological treatment of the penes as an index to the phylogeny in this genus.

When Gould described *columbianus* he clearly pointed out that it was a dimorphic species as indicated by his words, "there can be no doubt that the mottled animals are varieties of the uniformly colored ones, because they were not only taken in company, but in coitu." His term "varieties" can safely be construed to mean "color varieties." In spite of this, the literature was destined to be confused with names for the various color forms. Binney (1890) announced that Cockerell had suggested for the maculate form "the varietal name *maculatus*" thus unwittingly becoming author of this name. A year later, Cockerell published this name as *Ariolimax columbianus* forma *maculatus* and designated the immaculate form, which Gould considered typical, forma *typicus*. A unique black specimen was considered still different and was given the name forma *niger*. This should not be confused with *Ariolimax niger* Cooper 1872, which Simroth (1891) put in *Hesperarion*. Professor Cockerell was at that time working with specimens in the British Museum and unfortunately was not permitted to examine the specimens internally thus he was stimulated to put a too great emphasis on the external differences which, as stated above, have proven almost wholly unreliable. Pilsbry and Vanatta (1896) explained the status of "forma" as not being varietal or subspecific in nature and placed these names in synonymy. Cockerell (1897) did not attempt to resurrect these names. None the less, *maculatus* still persisted in the literature but without the word "forma" hence apparently assuming the status of a subspecies. Heynemann (1909), Craig (1927), Henderson (1927, '29) and others have perpetuated the name in this fashion.

For Cockerell's *A. columbianus californicus maculatus* see discussion under remarks for *californicus*.

A great many maculate and immaculate specimens have been examined externally and internally by the writer and absolutely no difference of a correlative nature was found. An almost black specimen from Washington was examined and it proved to be typical *columbianus*. Many populations include

maculate and immaculate individuals with all intergradations; this is especially the case in southern populations, e.g., on the University of California campus, Berkeley, California. Experiments are now in progress to determine the nature of this dimorphism.

In 1880 Wetherby found specimens sent to him from Santa Cruz, California, to be quite different and in spite of the fact that, upon examination of a specimen, Binney recognized it as a new species, Wetherby reported it *pro tempore* as *var. hecoxi* of *columbianus* giving no characters by which it could be identified. Binney (1885), out of deference to Wetherby, reported only the radula formula (which is not diagnostic in this genus), with the statement, "The genitalia examined by me proved the species to be distinct from any described." Subsequently, this *nomen nudum* appeared in the category of spurious and doubtful species pending a description.

Pilsbry and Vanatta in their revision of North American Slugs (1896), report the finding of a new ariolimacoid slug which differed from the described ariolimacines in three essential features, *viz.*, the complete absence of a penis and its retractor, the presence of a short epiphallus, and the location of the right tentacular retractor to the left of the genitalia. On the strength of these strikingly different characters, the new genus *Aphallarion* was founded. This genus existed without challenge for twenty years during which time the name *Aphallarion buttoni* found its way into the literature both in this country and in Europe. In 1916 Heath presented some rather startling information in his description of the loss of the penis of *A. californicus* during copulation. This information he presented to explain the reason he had found "that annually fully five per cent of the large-sized animals dissected in the classroom lacked the penis entirely." For all that he did not even hint the significance of this as regards the status of *A. buttoni,* Pilsbry assures the writer that since that time he has felt certain this latter was simply another ariolimacine which had similarly lost its penis. No published note has been made to this effect, however, probably because he was unable to discern, with the loss of the diagnostic penis, whether he had immaculate *columbianus* or *californicus*. Twenty-one years later Waste (1937) examined specimens from the type locality of *A. buttoni* (Oakland, California). He failed to find an aphallate specimen there but he stated that he had seen the aphallate condition in *californicus*. By a comparison of the extrinsic muscles of the vaginae, he was able to decide that *A. buttoni* was described from aphallate *columbianus;* he, therefore, put it into direct synonymy with the latter. Waste's work, though, is unfortunately hidden away at the University of California in a master's thesis; there thus exists to date no published clarification of this matter.

The type locality was carefully rechecked by the writer and aphallate specimens were found right along with normal *columbianus* differing significantly in no other respect. It was also found that *californicus* does not appear east of San Francisco Bay. Further, the specimen figured by Pilsbry and Vanatta (1896, pl. xiv, fig. 12) is obviously *columbianus* as it possesses the

characteristically long free oviduct; there is thus no doubt *buttoni* was described from aphallate *columbianus*. Apophallation alone accounts for most of the differences which Pilsbry and Vanatta found. The retractor of the right tentacle in *Ariolimax* normally passes between the penis and the vagina and is thus normally to the *left* of the vagina. The differences (P. & V. 1898) in the intestine and retentor muscle are within the range of normal variation and both the auricle and ventricle have always been fully concealed in the kidney in every one of several hundred specimens examined in this genus.

Heath, however, has not been so certain of this. He states (*in litt.*),

> .... since *A. californicus* loses this organ during copulation, it is generally believed that this invalidates Pilsbry's genus. However, years ago I visited Hog Island in Tomales Bay, and found over 400 specimens of what I thought was *californicus*. These were to be used for class work, but every one of the specimens was totally lacking a penis or any sign of one. The genus *Aphallarion* may be valid.

This tiny island was recently carefully searched but no slugs were found. On the adjacent mainland, however, immaculate *columbianus* were found in abundance among which were aphallate individuals. There is no doubt that Heath found this species and not *californicus* as is also apparent from the distribution of this latter. The significance of the 400 aphallate individuals, possible regeneration, cause of apophallation, and in fact the entire paradoxical genital physiological picture in this genus are to be treated in a subsequent paper. It is suffcient to state here that apaphallation has been observed by the writer, that it is of rather common occurrence in the genus, and that aphallate individuals are absolutely of no significance taxonomically.

But now let us return to *hecoxi*. Upon reading the description of *A. buttoni*, Wetherby recognized that the genital system of *hecoxi* was the same and Pilsbry and Vanatta (1890) were led to believe that the distribution of *buttoni* was thereby extended to Santa Cruz. *Hecoxi* was then (Pilsbry 1898a) placed in the synonymy of *columbianus*. Heynemann (1909) questioned this. With *buttoni* now in the synonymy of *columbianus* it would seem that the latter was found in Santa Cruz, but such is not the case. A study of the distribution of the genus has shown that not *columbianus* is found in that district but a new species. *Hecoxi* is thus an invalid name of the new species under which it is further discussed.

In 1900, Babor described *Ariolimax steindachneri* from a very large unique specimen collected at Puget Sound. His long dissertation on the characters of this specimen has been very carefully checked and but a single tangible character remains which would support his thesis that this species is intermediate between *Ariolimax* and *Hesperarion*. The other characters, too numerous to discuss here in their entirety, are largely based on intangibilities, natural variations to be expected within a species, and characteristics held in common by both genera concerned. A few characteristic examples will suffice here. He states that the suboral slime gland is intermediate as it is neither free nor embedded in the foot musculature but is entangled by "zahlreichen

losen dünnen Muskelbündeln." Such is the condition in every ariolimacine examined by the writer though it is not muscle bands but connective tissue which Babor saw.

His description of the penis could easily be that of *columbianus:* "Der Penis lang, schlauchförmig, ziemlich weit, gestreckt, oben unter der Anheftung des sehr kurzen und ausserordentlich dicken Retractors mit einer auffallend kurzen, dicken und konischen Ausstülpung versehen, welche eine niedrige, aber voluminöse Copulationspapilla enhält; sonst ist der Penis wohl leer. Er mündet nahe am unteren Ende des Oviductes in ein kleines Atrium genitale ein." Occasionally, a specimen improperly preserved will have the penis quite badly shrunken — even more so than the surrounding less elastic tissue. It is highly possible Babor had such a specimen and was giving too much emphasis to these severely dehydrated structures. There is also the possibility that he had an atypical specimen.

The same suggestion applies to his statement that the caudal slime gland was a slit without the filling of tissue (hence apparently linking it to *Hesperarion*). Live slugs put directly into alcohol or formalin will contract severely and such specimens are found to have withdrawn the thick plug of tissue thus bringing the caudal portion of the hollow foot close to the margin of the sole leaving but a slit.

But with these words in his discussion of the vagina, he clearly reveals the identity of this specimen, "der freie Oviduct ist ein grober, langer, muskulöser, walzenförmiger . . . Schlauch (ohne besondere Vaginalbildung), der nach einer kurzen knieartigen oberen Umbiegung in einigen leichten Spiraltouren verläuft." Such a description fits perfectly the condition in *columbianus* (*cf.* Figs. 5, 8, 14). Since the intrinsic muscle of the vagina is annular in *columbianus,* the vagina appears more or less tube-shaped indicating no special vaginal formation as in *californicus* (Figs. 1, 18). He has, however, considered the free oviduct and the shorter vagina together as the free oviduct itself. This explains the mysterious free oviduct retractor — it is merely the extrinsic muscle of the vagina which is found in all species of *Ariolimax* and is therefore nothing new.

His only tangible character is the absence of a retentor muscle. The absence of this is hard to explain. The writer has found it greatly reduced in size but in no case was it completely absent. At any rate, with all other characters, including size (*vide* Heynemann 1909), being applicable to a too quickly dehydrated specimen of *columbianus,* it does not seem advisable to consider this unique specimen a valid, distinct, and new species merely on the basis of the absence of a retentor muscle which might well be an anomaly or an oversight. It is for these reasons that *steindachneri* has been placed as a synonym of *columbianus* which is the only ariolimacine found in the district where it was collected.

Range.—At least as far north as "Sitka, Alaska, and probably north to Cross Sound and Icy Strait, or even Lituya Bay" (Dall, 1905) west of the

Cascade Range in British Columbia, Washington, and Oregon; into California south to Salinas Valley on the Coast and at least as far south on the western slopes of the Sierra Nevada as Tuolumne County.

California Distribution: ALAMEDA Co.: Berkeley§; Leona Heights (Ingram); Mills College§ (Ingram); Oakland§ (Cal. Acad. Sci. 11629, 11630) (P&V 1896); Strawberry Canyon§. BUTTE Co.: Chico (Waste). CALAVERAS Co.: Murphys§ (Baker, H. B.). CONTRA COSTA Co.: Orinda (Lange); Redwood Canyon Park (Lange, Ingram); St. Marys College (Ingram). DEL NORTE Co.: Hiouch St. Redwood Park (Chong); Redwood Hwy. Quar. Stn.§; Smith River (Lange). ELDORADO Co.: Riverton§. HUMBOLDT Co.: Carlotta (Lange); Ferndale (Storer); Fortuna (Bohart); Prairie Creek State Park (Lange). LAKE Co.: Clear Lake (Cooper 1873); Kelseyville (Lange); Lucerne (Keeble). MARIN Co.: Hog Island (Heath); Inverness§; Mt. Tamalpais St. Park (Morrow); Point Reyes (Lange); San Rafael (Lange); Sausalito Peninsula (Thompson). MENDOCINO Co.: Albion (Lange); Henry§; Mendocino City (Lange); Ukiah§; Westport§ (C.A.S. 11633). NAPA Co.: Knoxville§; Napa (Lange); St. Helena (Hemphill). PLACER Co.: Alta (Cooper 1886); Carpenter Flat (Lange). SAN FRANCISCO Co.: Pacheco St.§ (C.A.S. 29568); Sutro Forest§. SANTA CLARA Co.: Alum Rock Park§; Gilroy (Lange). SAN MATEO Co.: ?San Mateo (Binney 1874). SHASTA Co.: LaMoine (Lange). SOLANO Co.: Green Valley§. SONOMA Co.: Cazadero (Bohart). TRINITY Co.: Forest Glenn (Lange); Trinity Alps (Hanna). TUOLUMNE Co.: Columbia§ (C.A.S. 21500); Sonora§ (C.A.S. 21501). (Named after the Columbia River district.)

ARIOLIMAX COLUMBIANUS STRAMINEUS Hemphill
(Figs. 3, 13, 19)

Ariolimax columbianus [*partim, nec* Gould] Cooper, 1867:14.—Cooper, 1870:57.—Binney, 1878:231.—Binney, 1885:98.—Binney, 1890:211.—Waste, 1937:40.

Ariolimax columbianus [*nec* Gould] Yates, 1890:41.

Ariolimax californicus? Cooper, [*partim, nec* 1872] 1879:288.

Ariolimax californicus Cooper, [*nec* 1872] 1887:498.

Ariolimary [*sic**] *Columbianus* var. *straminea* Hemphill, 1891:120.

Ariolimax columbianus stramineus Cockerell, 1893:192.—Pilsbry & Vanatta, 1896: 344, 346.—Pilsbry, 1898:139.—Dall, 1905:48.—Heynemann, 1909:23, 25.—Keep and Baily, 1935:296.

Ariolimax hecoxi‡ [*nec* Wetherby 1880] Cooper, 1894.

Ariolimax columbianus straminea Orcutt, 1915:110.

Ariolimax columbianus columbianus [*partim, nec* Gould] Henderson, 1929:108.

External.—Ground color vitreous, lemon yellow or light straw-yellow; mantle concolorous. Longitudinal striae variable in number, concolorous and obscure; cross striae transverse or oblique, sparse and obsolete. Sole slightly wider than back; lateral striate portion moderately or contrastingly darker; concolorous, dusky, or slightly paler beneath with lateral thirds either concolorous or moderately darker than median third. Medium sized, slender; adults 20-25 gms. up to 27 gms.; foot length when fully extended 130-160 mm.

Genitalia.—Penis, retractor and ejaculatory duct similar to *columbianus* but penis always slender and apex of papilla not modified into a "glans."

§ Specimens examined from this locality.
* Correctly listed as Ariolimax in index to vol.
‡ Name cited in error.

Vagina a very long slender, cylindrical, straight tube nearly equal to or even exceeding penis length; basal portion usually thin walled, apical portion thick walled; intrinsic muscle obsolete or if present, thin, small, annular, and indistinct. Extrinsic muscle of vagina with insertion along median longitudinal axis of diaphragm; few fibers may unite with those of the retractor muscle of the penis. Spermatheca petiole extremely attenuate connecting broadly with vagina so that this latter appears to bifurcate. Free oviduct very short, cylindrical, and unmodified; its length shorter than that of vagina, usually much more so, and equal to or less than that of spermatheca petiole.

Syntypes.—Calif. Acad. Sci. nos. 2317-2320.

Type Locality.—"Santa Cruz Island, Calif."

Remarks.—Externally, this subspecies more closely resembles *dolichophallus* than true *columbianus*. It is unlike the latter because it is a smaller, more slender slug which is never maculate; it is always a light, bright yellow color and this does not vary greatly from population to population as it does in the polychromatic parent species.

The differences in the genital systems of *stramineus* and *columbianus* rest mainly in the female structures though the penis is different in that it is never heavy and massive. The long, slender, evenly cylindrical vagina, the absence or only slight evidence of an intrinsic muscle, the very attenuate spermatheca petiole with its base broadly joining the vagina, and the abbreviated free oviduct which is never long and modified, readily distinguish this subspecies. Some specimens of *columbianus* approach this subspecies in one or more respects but, of course, some intergradation is to be expected between subspecies. The external and internal differences plus the fact, as is discussed below, that the distribution is distinct amply vouch for setting aside this southern, more primitive, diminutive *columbianus* as a distinct subspecies.

Cooper made no special record as to when he first found *Ariolimax* as far south as Santa Barbara. This locality record shows up for the first time in 1867 in his statement of the range for the entire genus under the heading of *columbianus*, the only described species at that time. We now know this to be the first record for *stramineus*. This range ("Str. Fuca to Santa Barbara") was subsequently repeated several times (Cooper, 1870; Binney, 1878, etc.).

Cooper later (1879), in reviewing and criticizing Binney's work (1878) states, "In quoting my locality of Santa Barbara for *A. columbianus* Mr. Binney does not consider that I afterwards separated *A. californicus* from that species, and that the extreme southern specimens are more likely to be the latter, if not a new form." Binney (1885), however, disregarded this statement. Cooper still later (1887) followed his own suggestion and identified specimens collected "between Monterey and Carmel Bays" as *A. californicus*. An examination of material near this district shows that it is *stramineus* and not *californicus* which is found there.

Yates (1890) found an *Ariolimax* "quite common in El Montecito," Santa Barbara County, thus making the first definite report this far south for the genus. This he determined as *columbianus*.

Just a year later, Hemphill described from Santa Cruz Island, California, the new subspecies *straminea* of *columbianus*. The description was very abbreviated and concerned only four external characters — the "straw color" being the only one apparently diagnostic. This subspecies was not linked with continental populations in that latitude.

Cockerell (1893) changed the gender of *straminea* to agree with the rest of the name. This is desirable and thoroughly within the regulations of the international rules.

Pilsbry and Vanatta (1896:344) cite *stramineus* in the synonymy of *columbianus* and yet treat it as a valid "variety" (*l. c.* p. 346) with the simple statement, "Genitalia as in typical *A. columbianus*." Pilsbry gives it valid status in his check list (1898a). The fact that this subspecies represented an island population seemed sufficient to retain it as a distinct entity. Subsequent workers (Dall, 1905; Heynemann, 1909; Henderson, 1929, etc.) vary in their interpretations regarding this.

A comparison of specimens from the Santa Barbara Islands with those of coastal southern California indicates that they are identical and subspecifically distinct from true *columbianus* of more northern populations. *Stramineus* has thus hereby been redescribed and redefined.

Range.—Coastal California south and west of Salinas Valley from Monterey Peninsula to at least Ventura County, Santa Cruz Island, and Santa Rosa Island.

California Distribution: MONTEREY CO.: Big Creek§ (Lange); Big Sur State Park§ (Kantor, Lange); Hastings Reservation (Waste, Cal. Acad. Sci. 30905); Salinas Valley (Flock); Vincente Creek (Lange); "Between Monterey and Carmel Bays" (Cooper 1887); "20 mi. n. of San Simeon" (Lange). SAN LUIS OBISPO CO.: Little Pico Creek (Lange). SANTA BARBARA CO.: Cuyama Valley Road (Hanna, C.A.S. 27635); El Montecito (Yates); Santa Barbara (Cooper 1867 etc.). SANTA CRUZ ISLAND: Pelican Cañon§ (Kanakoff); Rockslide Cañon§ (Kanakoff); "Santa Cruz Island"§ (C.A.S. 11631, 2317-2320). SANTA ROSA ISLAND: Water Cañon§ (Kanakoff). VENTURA CO.: Santa Paula§ (Keene). (Lat. *stramineus*, straw-colored.)

Ariolimax dolichophallus n. sp.

(Figs. 4, 15, 16, 23)

Ariolimax columbianus [*partim nec* Gould] ?Cooper, 1867:14.—?Cooper, 1870:57.—?Binney, 1878:231.—?Binney, 1885:98.—Dall, 1905:47.—Waste, 1937:40.

Ariolimax columbiana [*sic*] var. *hecoxi* [*nomen nudum*] Wetherby, 1880:38.—Pilsby & Vanatta, 1896:347.

Ariolimax Hecoxi [*nomen nudum*] Binney, 1885:103.—Cockerell, 1890:279.—Cooper, [*partim*] 1894.

Ariolimax columbianus var. *Heacoxi* [*nomen nudum*] Heynemann, 1885:271, 315.

Ariolimax californicus [*nec* Cooper 1872] Cooper, 1887:?497, 500.—Cockerell, [*partim*] 1897:76.—Pilsbry, [*partim*] 1898:139.

Ariolimax columbianus var. *hecoxi* [*nomen nudum*] Cockerell, 1893:192.—Heynemann, 1909:23.

Aphallarion buttoni [*partim* nec P. & V. 1896] Pilsbry & Vanatta, 1898:236.—Pilsbry, 1898:139.

External.—Ground color opaque butter yellow; mantle concolorous. Longitudinal striae variable in number and very slightly darker in color; cross striae transverse or oblique, sparse and obsolete. Sole slightly wider than back; lateral striate portion moderate to contrastingly darker; concolorous, dusky, or somewhat lighter beneath with lateral thirds usually concolorous with, or at most slightly darker than median third. Medium sized, very slender; adults 20-25 gms. up to 39 gms.; foot length when fully extended 150-180 mm.

Genitalia.—Penis a hollow, flagelliform, extremely attenuate tube 60-110 mm. in length when relaxed and fully invaginated. The enlarged basal portion, with thick, muscular, internally plicate walls, quickly but not abruptly tapered to a fistular, flagelliform apical portion 2 to 4 times the length of the basal portion; apex tuberiferous. Vas deferens in basal region of penis enlarged to form a short, small ejaculatory duct, in width 1/4 to 1/3 that of greatest penis diameter; in length much less than that of penis from atrium to retractor muscle origin; this tapers rather abruptly into an apical vas deferens which quickly comes in juxtaposition to penis and soon broadly fuses with it but remains distinct in outline; in this manner it follows a long, straight path and empties into the penis close to its apex. Retractor muscle of the penis strap-shaped not flabellate; origin on penis at basal 1/3 to 1/4, insertion on diaphragm anterior or anterio-lateral to aorta. Vagina short, curvate, basal portion thin walled, apical portion thick walled; intrinsic muscle relatively small, flat, and considerably longer on right side but not projecting from general curvature of vaginal tube. Extrinsic muscle of vagina thin and long with origin from intrinsic muscle to spermatheca; insertion along median longitudinal axis of diaphragm; few fibers may unite with those of the retractor muscle of the penis. Spermatheca apical to intrinsic muscle by about the width of the vagina; low and sessile. Free oviduct relatively short, cylindrical and unmodified. Genital atrium shallow.

Types.—Holotype and one paratype in the California Academy of Sciences, and two paratypes each in the Academy of Natural Sciences of Philadelphia, the invertebrate collection of Cornell University, and the writer's collection.

Type Locality.—Saratoga, Santa Clara County, California.

Remarks.—This new species is immediately identified by the extremely attenuate apical phallus which not infrequently is of greater length than the slug itself! Even though with agitation or preservation it may contract considerably, it still remains proportionately much longer than that of *californicus* or its subspecies. The narrow retractor muscle of the penis, the reduced intrinsic muscle of the vagina, and the diagnostic small, short ejaculatory duct, as is shown in greater detail below, clearly reflect *columbianus* affinities.

On the other hand, the completely invaginated penis, the sessile spermatheca, and the form of the intrinsic muscle of the vagina indicate a more close relationship to *californicus* and in particular its subspecies with its diminutive genital structures. There is, however, no intergradation with these latter. Since it remains absolutely distinct and in addition has characters similar to those of *columbianus,* it is hereby described as a new species.

As pointed out under the discussion of *columbianus* above, Wetherby in 1880, believed the specimens he had received from Santa Cruz, California, were distinct; but unfortunately he published only the name of the animal, with the intention of publishing the description later, thus establishing a *nomen nudum* and the first authentic record of this species. For an unknown reason, he gave it a varietal name under *columbianus.*

We can interpret his informing Pilsbry (P. & V. 1898; P. 1898a) that his *A. columbianus hecoxi* was the same as *Aphallarion buttoni* to mean that he had aphallate specimen of this new species. It is little wonder then that he knew he had something distinct and that Binney, upon examining a specimen, "unhesitatingly" pronounced it a new species. But unfortunately the similarity was more apparent than real for with the diagnostic penis wanting, unless the relatively slight differences in the vaginae were known, they would seem identical except for body color which is not apparent in preserved specimens. From that time to date *hecoxi* has thus rested as a mere name in the synonymy of *buttoni* which latter has been clearly shown above to be synonymous with true *columbianus.*

Cooper (1887) reported finding this species "near the town of Santa Cruz" California, but he did not recognize that it was a different species than what had been described. Even though Binney (1874, '78, '85) had shown the differences in the genital system of *californicus* and *columbianus,* Cooper still relied wholly upon color differences to distinguish these species. Had he been in the habit of dissecting his material for determination, he well might have recognized this distinct species which externally greatly resembles *californicus.*

Pilsbry accepted this Santa Cruz record for *californicus* as valid and in his check list (1898) he accordingly extended the range of this species. Thus we have Pilsbry reporting *Aphallarion buttoni* and *Ariolimax californicus* from Santa Cruz. A survey of Santa Cruz County, however, revealed that only the new species was present and that aphallate specimens were very common. Apophallation has been observed in this species. We now know that Cooper's "*californicus*" and Wetherby's *hecoxi* are synonymous with the new species, that *hecoxi* only superficially resembled *buttoni,* and that these two latter names were both given to aphallate individuals of different species.

Wetherby points out that *hecoxi* ". . . may be the form referred to by Dr. Cooper as possibly new, in his review of Mr. Binney's Terrestrial Mollusks. . . ." Cooper, however, was referring to *stramineus* (*q. v.*).

Not only Wetherby and Cooper failed to recognize and describe this new species but Cockerell himself, who had distinguished and given names to color differences in *columbianus,* had two specimens in his very hands and yet did not recognize that they were specifically different from *californicus,* several typical drawings of which he had examined at that time (1897). He even cites two diagnostic characters with the statement, ". . . agree with those of Messrs. Pilsbry and Vanatta, except the epiphallus is less swollen and the retractor penis is not so broad." The locality record (Los Gatos, California) likewise identifies these as of the new species and not *californicus.*

At first, it would seem best to use Wetherby's name *hecoxi* as a name for this species and yet it would obviously only add to the confusion for he cited this name as a variety of *columbianus* before he had adequately studied the specimens. Moreover, he agreed that it was conspecific with *Aphallarion buttoni* which itself is of invalid status. But what is of even greater importance, he presumably had aphallate specimens which therefore lacked the structures wherein lay the most significant characteristics. It is for these reasons that the name *dolichophallus* has been selected which more suitably indicates the most characteristic feature.

It is not known whether Cooper (1867 etc.) included records of this species in his incorrect statement of the range of *columbianus viz.,* "Str. Fuca to Santa Barbara."

Range.—Limited to Coastal Central California from northern Santa Cruz and western Santa Clara south to Salinas Valley.

California Distribution: SANTA CLARA CO.: Congress Springs§; Los Gatos (Cockerell 1897). SANTA CRUZ CO.: Big Basin§; Big Trees§; Boulder Creek§; Brookdale (Heath); Chemeketa§; Hecker Pass§ (Lange); Mt. Hermon§; Santa Cruz (Wetherby 1880, Cooper 1887). (δολιχός-φαλλός, long phallus.)

ARIOLIMAX CALIFORNICUS Cooper

(Figs. 1, 18, 25)

Ariolimax columbianus [*partim nec* Gould] ?Cooper, 1867:14.—?Cooper, 1870:57.—Binney, 1878:231.—Binney, 1885:98.—Dall, 1905:47.

Ariolimax californicus Cooper, [*partim*†] 1872:146, pl. iii, fig. D, 1-3.—Binney, 1873:192, 198, 200.—Binney, 1874:33-38, pl. xi, fig. D-G.—Bland & Binney, 1874:297, 300†.—Binney, 1878:19, 21, 232, pl. v. fig. F; pl. xii, fig. D; text figs. 131, 132.—Binney, 1879:344.—Cooper, [*partim*] 1879:288.—Binney, 1883:162.—Binney, 1885:20, 23, 47, 99†, figs. 62, 63.—Heynemann, 1885:269, 271, 315.—Tryon, 1885:246.—Binney, 1886:43.—Cooper, 1887:367.—Pilsbry, 1889:199.—Binney, 1890:211, pl. v. figs. E, H.—Cockerell, 1890:278-279.—Simroth, 1891a:114, pl. i, 5,6.—Simroth, 1891b:365, pl. 7, figs. 9-11.—Cooper, [*partim*] 1894.—Pilsbry & Vanatta, 1896:346, pl. xiii, figs. 5, 6; pl. xiv, figs. 13-16.—Cockerell, [*partim*] 1897:76.—Pilsbry, [*partim*] 1898:139.—Gratacap, 1901:370.—Raymond, 1903:9.—Heynemann, 1909:23, 25.—Orcutt, 1915:54.—Heath, 1916:22-24.—Simroth & Hoffmann, 1928:525, fig. 171, F.—Henderson, 1929:108.—Keep & Baily, 1935:296.—Waste, [*partim*] 1937:45, pl. 1, fig. 1; pl. 6, fig. 1.

Ariolimax var. *Californicus* Cooper, 1872:154.

† *Nec* Sierra Nevada reference.

Ariolimax californicus v. *columbianus* Simroth, 1891a:111.

Ariolimax columbianus californicus Cockerell, 1893:192.

[*non Ariolimax californicus* Cooper, 1876:24.—Cooper, 1886:253.—Cooper, 1887: 367 (Sierra Nevada ref. only), 370, 372, 373, 375, 497, 498, 500, 502, 503, 506.—Cooper, 1890:70.—Wood and Raymond, 1891:56.]

[*non Ariolimax* subsp. *Californicus* forma *maculatus* Cockerell, 1891:31 (foot note).]

[*non Ariolimax columbianus californicus maculatus* Cockerell, 1893:192.—Cockerell, 1897:76, 77.]

External.—Ground color vitreous butter yellow, rarely ochraceous yellow; mantle concolorous, rarely lighter. Longitudinal striae variable in number and slightly darker; cross striae transverse or oblique prominent or obsolescent. Sole moderately wider than back; lateral striate portion concolorous or less often somewhat darker; concolorous or slightly lighter beneath with lateral thirds concolorous or slightly darker than median third. Large, robust; adults 25-35 gms. up to 42 gms.; foot length when fully extended 175-200 mm.

Genitalia.—Penis a large, hollow, robust, elongate tube 50 to 73 mm. in length when relaxed and fully invaginated. The enlarged basal portion with extremely thick, muscular, internally plicate walls, gradually tapering to a sender apical portion 1 to 1½ times the length of the basal portion; apex slender and irregular or smooth and clavate. Vas deferens in basal region of penis quickly enlarged to form a very long, cylindrical, large ejaculatory duct, in width ½ to ⅞ that of greatest penis diameter; in length considerably exceeding that of penis from atrium to retractor muscle origin; this tapers rather abruptly into a distal vas deferens closely connected to apical penis by connective tissue, not becoming broadly fused but remaining quite distinct as it passes tortuously toward the apex; after fusing for a short distance, it empties into the penis close to its apex. Retractor muscle of the penis broadly flabellate; origin very broad on penis so that the most apical point of attachment to penis is about midway between apex and atrium; insertion extremely broad on body wall posterior or posterio-lateral to aorta. Vagina short, basal portion thin walled, apical portion almost completely obscured by the very large, flat, discoid intrinsic muscle which greatly extends the right side of the vagina and encroaches upon its lumen. The intrinsic muscle is heaviest in a right crescentic band and in tubercules facing the lumen. Extrinsic muscle of vagina short with origin from intrinsic muscle to spermatheca; insertion along median longitudinal axis of diaphragm. Spermatheca immediately apical to intrinsic muscle; low and sessile. Free oviduct relatively short, cylindrical and unmodified. Genital atrium shallow.

Types.—Unknown.

Type Locality.—"Coast range" (see remarks).

Remarks.—This species is the second largest in the genus but possesses by far the largest and heaviest genital structures. It would be confused only with its subspecies; the differences between these two are discussed under the latter (*q. v.*). The significance of the general great increase in the genital musculature is treated below in the discussion of the homologies of the penes.

It is indeed unfortunate that Cooper continually relied entirely upon highly variable external characters for determining slug species. His description (1872) of this species amply manifests the confusion which arises with such a procedure. In his description he mentions but two characters, by which this species could supposedly be distinguished from *columbianus, viz.*, the much more frequent dorsal grooves or striae and the transverse position of the connecting reticulations or cross striae. Both of these characters are highly variable and are therefore completely worthless in identifying species. No internal characters were given.

It is not quite clear what status he intended giving this new entity for he not only places an interrogation mark after name *californicus* but he states, apparently realizing the variable nature of the characters given, ". . . and, did I not find considerable variation among them, I would consider it certainly a different species." This statement is given further significance when one notes in his explanation of the plates that he lists the figures as "*Ariolimax* var. *Californicus*," thus indicating that he considered it merely a variety of *columbianus*. He also uses the word "variety" in the text of his description (*l. c.*, p. 147, line 4).

His confusion is made even more apparent when it is noted that in this description he was still unable to correctly distinguish between *californicus* and *columbianus*, for he stated, "Mr. Voy has brought it from the Sierra Nevada, lat. 39°, alt. about 3500 feet, but I have not heard of it elsewhere out of the coast range." Specimens collected in the Sierra Nevada by the writer prove to be immaculate *columbianus*. This leaves the name *californicus* practically meaningless. We are not justified in discarding it, however, for Binney (1874) showed that there existed a considerable difference in the genitalia of *columbianus* and what he determined as *californicus*. It is interesting to note at this point that it was by the luckiest accident that Binney happened to identify correctly the two specimens he had from San Mateo County—one *columbianus* and one *californicus*. One of the specimens seemed to have individual male and female genital orifices and since this seemed to be the case in the specimen figured by Cooper (1872), he decided it was *californicus*. Since the other specimen was different internally and had but a single genital orifice, he decided it had to be *columbianus*, his uncertainty being indicated by an interrogation mark after his name. He later (1876) examined material from farther north and thus removed all doubt that he had had in 1874 true *columbianus*. Most subsequent workers, knowing these internal differences, accepted *californicus* as a full-fledged respectable species.

Since we now know that *californicus* is not found in the Sierra Nevada, and to avoid greater confusion, it will be well to disregard Cooper's mistake here and consider the locality "coast range" as being the home of his species. Binney's specimen came from San Mateo which is in the "coast range." Pilsbry and Vanatta (1896) describing in detail the external and internal anatomy, also had specimens from the same locality. Specimens from the western foothills adjacent to San Mateo have been examined by the writer

and they have been found to be typical. This now begins to properly define *californicus*. It is unfortunate though, that Cooper's Sierra Nevada citation showed up several times in the literature (B. & B. 1874; Binney, 1885 etc.). It is likewise unfortunate that Binney's incorrect interpretation of the genital orifice of this species was perpetuated by him in his subsequent works (1878, '85). At that time, it appeared that the two species could be distinguished simply by the double or single nature of the genital orifice. Simroth (1891b), however, showed Binney to be in error and indicated the orifice of *californicus* to be single in nature.

Cooper may have earlier (1867, '70) included populations of this species in his statement of the range of *columbianus* ("Str. Fuca to Santa Barbara"), but there is no way of discerning this as he made no itemization of the localities where he had collected *Ariolimax*. With Binney's work on the internal anatomy long in print, Cooper should not have continued to confuse these two species (1876, '86, '87, '90). For example, as late as 1886 he states regarding an *Ariolimax* which he collected in the Sierra Nevada and identified as *californicus*, ". . . apparently identical with the coast species." This manifestly indicates that his concept of his own species was not at all clear; he did consider *californicus* in these later writings, however, as a species and not a variety.

On the other hand, Cockerell was not so certain whether he should call *californicus* a subspecies (1891, '93) or a species (1890, '97). The real confusion came when he examined (*vide* 1897) two maculated specimens from Binney in the British Museum one of which was identified as *californicus* and the other *columbianus*. From these two, he not only concluded that the two species were "hardly to be separated as species" (1890), but that *californicus* possessed a maculate form as well. To this latter he gave the name *Ariolimax* subsp. *Californicus* forma *maculatus*. Pilsbry and Vanatta correctly assumed (1896) that this latter was "identical with the spotted form of *columbianus*." Even though Cockerell was not permitted to dissect these specimens, he should have exercised extreme caution in giving such a name solely on the basis of external characters especially since Binney (1874) had shown the importance of internal characters.

Tryon likewise was uncertain as to the status of *californicus* (1885) for he states regarding it, ". . . nevertheless it may prove to be a variety of that [*columbianus*] species." It is hard to understand why he makes this statement in the face of Binney's work which amply shows more than varietal difference to exist in the genitalia.

The same remarks apply to Simroth (1891b) who, influenced by Cockerell, refers to a specimen by the hybrid name, *Ariolimax californicus* v. *columbianus* (which according to his description is true *californicus*) and makes the statements, ". . . sonst kaum zu trennenden Species *Ar. californicus* und *columbianus*," and, ". . . wohl identisch."

For all that the aforesaid work of Binney was very important and significant, many of his interpretations were incorrect. Pilsbry and Vanatta (1896)

corrected most of these; consequently only those matters which still remain as misinterpretations will be treated here. Binney interprets the large "ear-shaped" organ of the female conduit near the genital orifice as a "vaginal prostate." Pilsbry and Vanatta were more observing but no more correct as they refer to it as a "broad, stout, fleshy vaginal retractor muscle" and so indicate it in their illustration. Upon closer examination, it can be seen that this fleshy mass is entirely within the vaginal wall and is therefore the *intrinsic* muscle of the vagina. It has been shown above that the shape of this intrinsic muscle is of taxonomic importance and it will be further shown that it plays an imporant part in apophallation. The extrinsic muscle of the vagina or the so-called retractor muscle is, on the other hand, extremely reduced in adult specimens of this species as the intrinsic muscle has developed to such an extent that it comes in close proximity to the insertion of the extrinsic muscle; hence, if this latter is to function at all, it must be very short — as it is (*cf.* that of *columbianus*).

Binney (1874) referred to the apical portion of the penis as the flagellum, though he later (1878, '85) states that the vas deferens "enters the penis at the end of the flagellum below the bulb." Simroth (1891b) pointed out that this structure is a part of the penis itself and not a separate structure as, for example, in *Helix*. He further pointed out that Binney was not correct in assuming that "the penis is enclosed in a long, tapering sac" by stating, "es ist der Schlauch selbst, der den Namen verdient." The large, globular bulb on the end of the "flagellum" of Binney's specimen (1874, pl. xi, D) did not show up in Simroth's specimen. This is not a separate structure but a highly distensible apical portion of the penis which has been observed, in anesthetized specimens, to distend and contract completely at irregular intervals. The specimen illustrated by Pilsbry and Vanatta, on the other hand, was apically invaginated and this they misinterpreted. Waste (1937) followed their interpretation. This invagination, its interpretation, its significance; the so-called "epiphallus," its function, its significance; and the general relationships of these male structures are treated below in the discussion of the penial homologies.

Range.—Limited to San Mateo and northwestern Santa Clara Counties in Coastal Central California.

California Distribution: SANTA CLARA CO.: Stanford University§. SAN MATEO CO.: Half Moon Bay§ (Waste, Lange, Cal. Acad. Sci 30904); La Honda§; Lake San Andreas§; Pescadero (Flock); San Francisquito Creek (Heath); San Mateo Co. (C.A.S. 11632); Woodside (Flock).

Ariolimax californicus brachyphallus n. subsp.

(Figs. 2, 17, 24)

Ariolimax columbianus [*partim nec* Gould] ?Cooper, 1867:14.—?Cooper, 1870:57.—?Binney, 1878:231.—?Binney, 1885:98.—?Dall, 1905:47.

Ariolimax californicus [*nec* Cooper 1872] ?*Cooper, 1887:502, 503(4th line).—?*Wood & Raymond, 1891:56.—Waste, [*partim*] 1937:46.

* May have been immaculate *A. columbianus*.

External.—Ground color ochraceous or ochraceous brown; mantle ochraceous yellow, rarely concolorous. Longitudinal striae variable in number, darker in color; cross striae transverse or oblique, prominent. Sole slightly wider than back; lateral striate portion moderately darker; dark beneath with lateral thirds usually strikingly darker than median third. Small, moderately slender; adults 17-20 gms. up to 23 gms.; foot length when fully extended 125-150 mm.

Genitalia.—Penis a small, hollow, slender, elongate tube 30 to 42 mm. in length when relaxed and fully invaginated. The enlarged basal portion, with thick, muscular, internally plicate walls, very evenly and gradually tapering to a slender apical portion 1 1/3 to 1 2/3 times the length of the basal portion; apex slender and irregular or smooth and clavate. Vas deferens in basal region of penis enlarged to form a long, large ejaculatory duct, in width ½ to ¾ that of greatest penis diameter; in length considerably exceeding that of penis from atrium to retractor muscle origin; this tapers into an apical vas deferens which is essentially similar to that of *californicus*. Retractor muscle of penis broadly strap-shaped or somewhat flabellate but not broadly so; origin on penis at basal 2/5 to 3/8; insertion on body wall immediately posterior or posterio-lateral to aorta. Vagina short and broadly curvate or nearly straight; basal portion thin walled; apical portion thick walled and very short; intrinsic muscle located on right side, small, quite thick, trilobate, and cylindric or subdiscoid; not or slightly extending to the right the general curvature of the vaginal tube. Extrinsic muscle of vagina thin and long with origin from intrinsic muscle to spermatheca; strands converge to insertion near central diaphragm. Spermatheca basal and close to intrinsic muscle; low and sessile. Free oviduct and genital atrium as in *californicus*.

Types.—Holotype and one paratype in the California Academy of Sciences, and two paratypes each in the Academy of Natural Sciences of Philadelphia, the invertebrate collection of Cornell University, and the writer's collection.

Type Locality.—Mt. Davidson, San Francisco, California.

Remarks.—This subspecies is the smallest in the genus. It will be rather difficult to separate from its parent species unless full grown adults of the latter are at hand. This is especially the case with specimens of *californicus* which have undergone seasonal atrophy of the genital system after the first winter of sexual maturity. The shorter and more slender penis, the smaller ejaculatory duct, the more slender retractor muscle of the penis, and the smaller intrinsic muscle of the vagina are characteristic of full grown sexually mature specimens of this subspecies in the breeding season. As the illustrations show, these structures are in strong contrast with those of an equally mature specimen of *californicus*. The contrast, however, is mainly in degree for they are both built along the same fundamental plan. We can thus conclude that *brachyphallus* is a diminutive *californicus* and as shown below in the discussion of the penial homologies, it is in this respect more primitive. The significance of the small size and the less muscular nature of the genitalia

with regard to apophallation is also indicated. As will be pointed out in a later paper, the genital physiology of this subspecies is also strikingly different. These characters plus the fact that it is more or less isolated in San Francisco, will warrant designating it as a distinct subspecies.

It is possible that the first record of this subspecies was made by Cooper in 1887 when he reported "*californicus*" from San Francisco. Wood & Raymond (1891) made a similar report. Since immaculate *columbianus* is also found in that locality, they may have confused these two species. True *californicus*, however, is not found that far north.

Waste (1937) was first to make an authentic report of this subspecies though he did not recognize that it was different from true *californicus*.

Range.—Limited to San Francisco Peninsula, California.

California Distribution: SAN FRANCISCO CO.: Mt. Davidson§; Mt. Sutro§ (Cal. Acad. Sci. 29571). (*βραχύς-φαλλός*, short phallus.)

Doubtful Species

ARIOLIMAX CALIFORNICUS subsp. COSTARICENSIS.—This was described from a unique specimen in the British Museum by Cockerell (1890). As only a few external characters were given, the animal cannot be safely identified beyond Arionidae. Since he later (1893) considered *californicus* a subspecies of *columbianus*, he apparently lists *costaricensis* also as a subspecies of the latter. In 1897 he attempted to defend the attack upon this subspecies by Pilsbry and Vanatta (1896) by pointing out that he was not permitted to dissect the specimen and that they have overlooked "the peculiar olivaceous color." This color, of course, is neither peculiar to *californicus* nor the genus. He states further (*in litt.*), "There are three possibilities; (1) that dissection would show generic differences, (2) that the animal had been introduced from somewhere northward, (3) that the locality given was wrong." None of these is sufficient to warrant giving the animal the status it now possesses. The first possibility is the most probable as this record is completely out of the known range of the genus *Ariolimax*. A study of the biology of this genus indicates that the second possibility is indeed unlikely. Since this specimen cannot now be examined, it seems apparent that it should be given the status of *incertae sedis* with the understanding that it cannot rightfully take the status given it by Cockerell.

ARION EMPIRICORUM.—This European slug was reported by Grateloup (1855:8) from the "Les Etats-Unis de l'Ouest." Since the ariolimacines are the only American slugs which resemble this European cousin, it remains a possibility that he was actually reporting *Ariolimax* although he also reports in the same article (p. 14) *Limax Columbianus* from "États-Unis du N. et de l'O., la Colombie." Gould (1850) in his original description of the latter species indicated the great similarity to *A. empiricorum*.

There should be no confusion of *Ariolimax andersoni* Cooper as it has

been shown to be a synonym of *Ariolimax niger* Cooper which with *Ariolimax hemphilli* Binney has been placed in the genus *Hesperarion* by Simroth (1891a). Pratt (1935) and Keep & Bailey (1935) are not up to date on this.

Key

In this genus the species resemble each other more closely than in any other American slug genus, so much so in fact, that it is not possible to make a field key which would be at all practical. This is immediately apparent when one reads the description of the external characters of the several species. With the distribution of the species well known, this immediately becomes the most important means of identifying them in the field, and practically the only means by which very immature specimens can be identified. To be absolutely sure of the identification of an immaculate specimen from a new locality, however, one must examine the genitalia. The diagrams (Figs. 1-5) in addition to the key, based entirely upon the differences in the genitalia, should make it relatively easy to distinguish between these rather closely related species, especially if full grown and sexually mature specimens are used.

A Penis a permanently partially evaginated tube forming a thin walled sheath and an internal thick walled penis papilla; retractor muscle narrow and strap-shaped with origin on penis apex. Ejaculatory duct narrow, poorly defined, 2 to 3 times the diameter of the basal vas deferens. Intrinsic muscle of vagina small and annular or obsolete. Spermatheca petiolate.

B Penis robust or slender. Vagina short and squat, rarely elongate; intrinsic muscle thick and annular. Spermatheca petiole usually short and not exceeding free oviduct in length; base narrow. Free oviduct very long and convoluted, very wide and flat, or short and unmodified, equal to or usually much longer than vagina ..... *columbianus*

BB Penis slender. Vagina very long, slender, cylindrical, and straight; intrinsic muscle obsolete or indistinctly seen as a paler, poorly defined annulus. Spermatheca petiole attenuate, exceeding free oviduct in length, frequently considerably so; base almost as wide as free oviduct. Free oviduct short and unmodified, shorter than vagina, usually much more so..... *columbianus stramineus*

AA Penis a long hollow tube which can be completely invaginated; no differentiation into penis sheath and penis papilla though apex may be temorarily evaginated (especially in immature specimens) to simulate this condition; retractor muscle strap-shaped to broadly flabellate, origin on lateral penis. Ejaculatory duct well defined, 3-10 times the diameter of the basal vas deferens. Intrinsic muscle of vagina large, asymmetrical, and heavier on the right side. Spermatheca sessile.

B Apical portion of penis flagelliform, 2 to 4 times the length of basal portion; retractor muscle narrow and strap-shaped; insertion usually anterior or anterio-lateral to aorta. Ejaculatory duct shorter than basal penis and 1/4 to 1/3 the width of greatest penis diameter. Apical vas deferens straight and broadly connected to penis..... *dolichophallus*

BB Apical portion of penis slender, 1 to 1 2/3 times the length of basal portion; retractor muscle broadly strap-shaped to broadly flabellate; insertion usually posterior or posterio-lateral to aorta. Ejaculatory duct longer than basal penis and 1/2 to 7/8 the width of greatest penis diameter. Apical vas deferens tortuous and loosely connected to penis except in region of penis apex.

c Penis of adult large, robust and long, 50 to 73 mm. in length; retractor muscle broadly flabellate with apical point of origin on penis about equidistant from atrium to apex, origin very broad. Ejaculatory duct large and robust, ½ to ⅞ that of greatest penis diameter. Vagina with very large, heavy, flat, discoid intrinsic muscle greatly extending the right vagina wall. Extrinsic muscle of vagina short ..... *californicus*

cc Penis of adult small, slender, and short, 30 to 42 mm. in length; retractor muscle strap-shaped or slightly flabellate with apical point of origin on penis considerably below midpoint between atrium and apex, origin narrow to moderately broad. Ejaculatory duct smaller and more slender, ½ to ¾ that of greatest penis diameter. Vagina with small cylindric or sub-discoid intrinsic muscle not or slightly extending the right vagina wall. Extrinsic muscle of vagina long ..... *californicus brachyphallus*

Penial Homology as an Index to Phylogeny

The key to this whole subject was found by a careful study of the evagination of penes of the *californicus* type. Anesthetized specimens were stimulated to evert the penis and in this process the penial homologies, of the superficially very diverse *californicus* and *columbianus* types, became immediately apparent.

In sexually mature *californicus*, the penis is normally completely invaginated (Fig. 1). Fig. 9 represents an enlargement of the penis apex showing the point of entrance of the apical vas deferens. Evagination of the penis is initiated by the action of the antagonistic circular and longitudinal intrinsic muscles of the penis apex; this is augmented by a forward influx of blood increasing the pressure in this region. In freshly dissected specimens, the penis is often seen evaginating for a considerable ways or invaginating completely thus proving that blood pressure plays a minor role in the extroversion of the penis during copulation. As the arrows indicate (Fig. 10), the apex (*b*) folds within itself and carries with it the apical vas deferens (*av* Fig. 11). The same relationships are effected if one partially invaginates the finger of a rubber glove with, say, a piece of glass tubing. As the evaginated apex approaches the atrium, the region of active evagination is close to the origin of the retractor muscle (*rmp*). At this instant we have virtually the relationships which exist in *columbianus!* A longitudinal section of the penis of *columbianus* (Fig. 8) makes this apparent. The homologous structures can now be indicated.

The thin walled penis sheath (*ps*) of *columbianus* is homologous to the thicker walled basal penis (*bp*) of *californicus* which no longer functions as a sheath. The slender apical portion in *californicus* (*ap* Fig. 1) is now seen to be, when in the normal position, nothing more than the completely invaginated penis papilla (*pp*) of *columbianus*. In the latter species, however, the walls of the penis papilla are more primitively thick and when in the normal position are in close contact with the inner epithelial layer of the penis sheath which is apically continuous (*x*) with the papilla epithelial layer. The apex of the penis papilla (*g*) marks the apical extremity of the penial tube as it does in the so-called "penis apex" (*b*) of *californicus*. With the homology

of the parts now known, the currently accepted anatomical designations become ambiguous, for the *real* apex of *californicus* is in the region of the retractor muscle origin and the apparent penis apex (*b*) is really the invaginated apex of the penis papilla! The apices of the penial tubes in both types are homologically thin walled and highly distensible giving rise in *californicus* to the so-called "bulb" (*vide* remarks under this species) and in *columbianus* to the "glans."

The apical vas deferens (av^1) of *columbianus,* after passing through the broad origin of the retractor muscle, swells abruptly into a thin walled structure (av^2) increasing 3 to 4 times in diameter and then tapering gradually to its former diameter at its junction with the penis papilla. Between the inner wall of the penis papilla and this apical vas deferens is a loose webbing of connective tissue (*ct*) holding the latter along the median longitudinal axis of the papilla. In *californicus,* however, the apical vas deferens (*av*) has become slender throughout and only a small amount of the loose connective tissue (*ct*) remains to attach it to the apical penis. A slug of the *columbianus* type, if provided with a very restricted and laterally placed retractor muscle origin and an almost complete absence of binding connective tissue within the penis papilla, could presumably completely invaginate the papilla after the manner of *californicus.*

The swollen portion of the vas deferens (*e*) of *californicus* has been referred to by Pilsbry and Vanatta as the "epiphallus" — a term which does not commit itself as to the function of the organ. A series of transverse sections of this structure indicates that there is no increase in the lumen of the vas deferens but that there is an enormous increase in the musculature of the wall. The structure therefore is without any doubt ejaculatory in function; hence the name *ejaculatory duct* seems more appropriate and accordingly has been used herein. Simroth (1891b) observed that this structure, to which he gave the name "Patronenstrecke," was thick walled but he offered no suggestion as to its function. The current opinion is that it, like the flagellum of *Helix,* forms the spermatophores. The locus of this process in the spermatophore-forming arionids is perhaps indicated by the condition in *Hesperarion* (Fig. 7). In an anesthetized specimen examined, the vas deferens was found to swell apically into a glandular, thin walled portion (*a*) which became very thick walled (*e*) just before entering the penis apex. The former probably forms the spermatophores and the latter surely act as an ejaculatory duct. Contrary to the suggestions in the literature, *Ariolimax* does not form spermatophores. It is the opinion of the writer that most if not all of the members of this family possess "epiphalli" which are ejaculatory in nature; further investigations are in process to support this opinion. The thick walled "epiphallus" of *Prophysaon* (*vide* P. & V. 1898, pl. xiii, 55, 56) is undoubtedly largely if not entirely ejaculatory in nature.

Pilsbry and Vanatta (1896) cut open and examined the penis of *columbianus* and made interpretations which are not in accordance with the present investigation. Influenced by the work of Hedley, they believed the "inner

body" (or what is termed here the penis papilla) to be an "introverted epiphallus" and the atrial end of this structure to be the "penis papilla" (which is shown here to be the glans). Waste (1937) believed this structure within the penis sheath "to be formed from an internal growth of the sperm duct" and made the statement that it was not homologous with the "epiphallus" of *californicus*. He thus innovates the term "intraphallus." These investigators seem to have ignored the slightly swollen vas deferens adjacent to the penis. Had they cut this, they would have found a thicker walled conduit diminutive, but entirely homologous to the ejaculatory duct of *californicus* as it is morphologically in the same relative position. The "inner body" therefore cannot be called an "introverted epiphallus." With a knowledge of the homologies, there is little need for the new term "intraphallus" when the old term "penis papilla" is just as suitable.

A brief examination of these structures of *Hesperarion niger* will not only vouch for the suitability of the terms herein accepted, but will also throw light on the phylogeny. Due to the kindness of Dr. W. H. Lange, the author was able to obtain a full grown live specimen which was anesthetized and examined in the same manner as the *Ariolimax* material. Fig. 6 shows the penis sheath (*ps*) cut to expose the minute, short, conical penis papilla (*pp*) within. This latter and the modified apical vas deferens were cut and the relationships therein noted are depicted semi-diagrammatically in Fig. 7. The relationships are strikingly like *columbianus!* The penis papilla is formed by a permanently partially evaginated hollow tube, the largest portion of which forms the penis sheath whose walls are directly continuous apically (*x*) with the papilla. The apical vas deferens (av^2), however, is so short that the ejaculatory duct (*e*) is contiguous with the apical limits of the penis sheath, but like *columbianus,* it is apically large and thin walled, tapering to a narrow duct at its junction with the penis papilla. The loose connective tissue (*ct*) is similarly arranged and like that of *columbianus* combines with slips of the retractor muscle (*rmp*) obscuring the evaginated nature of the penis papilla. This papilla, heretofore, has been thought to be "solid" and "not invaginated."

To emphasize still further the great similarity in these seemingly very different penes, the mechanics of complete evagination, as in copulation, and the resultant intromittant organs will be described. In *californicus,* the everting process described above continues until finally the penis becomes completely evaginated and distended with blood (Fig. 12). The apical vas deferens, the ejaculatory duct, and a good share of the retractor muscle also are seen to have been carried out well beyond the normal confines of the body wall.

It will be seen that if the penis of *columbianus* were completely everted, essentially the same type of intromittant organ would be formed. It would have a somewhat thicker walled distal portion and a thinner walled proximal portion; the converse, of course, obtains in the *californicus* type. The plug of retractor muscle tissue and connective tissue of the former, contrary to all indications, does not effect a complete closure of the penis papilla cavity;

consequently, the distal end is just as effectively distended with blood as is the *californicus* type. This phenomenon was checked by pipetting normal saline into the everted penis.

The *Hesperarion* type, when completely everted, is remarkably similar, with the shorter distended penis papilla located distal to the long, cylindrical blood-filled penis sheath which, like the *californicus* type, is equipped with a somewhat more muscular basal portion (*m*, Fig. 6). Note that despite the fact that the ejaculatory duct is located more apically, like *columbianus* it is still contained within the distended walls of the penis sheath. The everted penis, therefore, does not resemble Pilsbry and Vanatta's diagram of *columbianus* (1898:345) as at first might seem to be the case. The *columbianus* type can be evolved from the *Hesperarion* type by either one of two processes. The ejaculatory duct would have to become basally displaced from the penis papilla with an accompanying increase in length of the unmodified apical vas deferens. The penis papilla would become longer either by a continued evagination of the sheath with a concomitant lengthening of the latter, or, what is much more probable, by simple intussusception with little or no change in the nature of the sheath.

The large ejaculatory duct of *A. californicus, brachyphallus,* and *H. niger* probably function incidentally as a support for the distended basal penis.

It is of significance to note that almost without fail, sexually immature specimens with the *californicus* type of penis have the apical penis evaginated almost as far basally as the retractor muscle origin, simulating somewhat the condition in *columbianus*. The penis of the adults, however, is normally completely invaginated but not infrequently it is found slightly evaginated. Pilsbry and Vanatta dissected a specimen of this sort and they assumed that this apparently distinct structure was an "introverted and invaginated epiphallus." On the other hand, immature specimens of *columbianus* possess a very abbreviated penis papilla and a very long penis sheath presenting a striking similarity to the condition in mature *Hesperarion*.

The phylogenetic relationships are now practically self-evident. The *Hesperarion* type is prototypic; the *columbianus* type is essentially an amplification with greater attenuation of the penis papilla; the *californicus* type is unfolded and invaginated with a reduction in the connective tissue and in the musculature of the penis papilla and with an increase in the musculature of the penis sheath. This interpretation is essentially the reverse of that of Pilsbry and Vanatta (1896).

Stramineus, with its diminutive genital structures, probably is the most primitive in the genus *Ariolimax*. *Columbianus* is only a little more advanced with generally a more robust penis, a well developed annular intrinsic muscle of the vagina, and a frequently very modified free oviduct. The remaining two species and one subspecies, are now known to be considerably more advanced. Of the three, which are quite closely related, *dolichophallus* indubitably stands as the most primitive, for the narrow strap-shaped retractor

muscle of the penis and the slender ejaculatory duct as well as the reduced intrinsic muscle of the vagina are not only very similar to those of *columbianus,* but are manifestly much less advanced than those of *californicus* or its subspecies. The genital structures of *brachyphallus,* with the exception of the apical penis, is of about the same caliber as *dolichophallus* and provides a nice connecting link in complexity between the latter and *californicus* with its very robust genital structures. Like *stramineus, brachyphallus* is a more primitive, diminutive edition of its parent species. In this series of three more advanced ariolimacines, the main theme of evolution has been the general increase in musculature of the genital structures. *Californicus,* with its voluminous retractor muscle, extremely large and thick walled penis and ejaculatory duct, and hypertrophied intrinsic muscle of the vagina, thus stands at the top representing the maximum in muscle development.

The details of apophallation, that is, the paradoxical act of gnawing off the penis as a culmination to copulation, will be treated, along with copulation and the genital physiology of this genus, in a later paper. It will suffice here to indicate that this phenomenon occurs in *columbianus* and has been observed in *dolichophallus* and *californicus.* Mechanical difficulty alone is responsible for apophallation though the nature of the difficulty varies with each species.

In *californicus* the lumen of the vagina has been seriously reduced by a tremendous development of the intrinsic muscle; as if this did not provide sufficient difficulty, the very large penis is made still larger with evagination when the almost equally large ejaculatory duct is incorporated. Since the intrinsic muscle clasps onto the penis during copulation, there is little wonder that the latter becomes so firmly fixed that apophallation must be resorted to in order to free the two individuals. *Brachyphallus,* on the other hand, apparently almost never needs to resort to such a drastic measure as its diminutive genital structures permit copulation with little or no difficulty. Out of a great number of individuals examined, only two were found in the aphallate condition; these specimens cannot be considered normal, however, as they were members of a large population experimentally held in prolonged unfavorable conditions. Nevertheless, apophallation may occur in nature in this subspecies but certainly not more frequently than an occasional rare case.

The mechanical difficulty in *dolichophallus* is incurred by the extremely attenuate apical penis which literally ties itself into a knot while in the spermatheca of its partner thereby inextricably anchoring itself. The thick walled basal penis and the intrinsic muscle probably contribute to the dilemma.

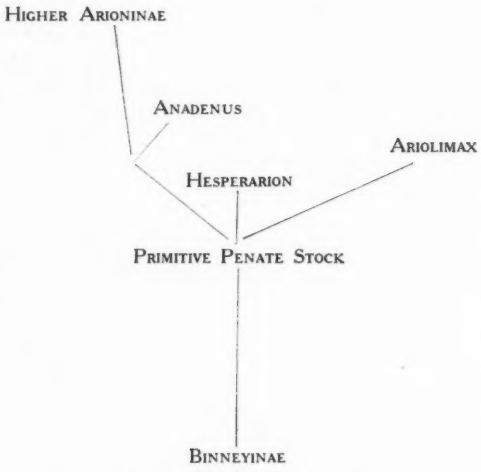
In *columbianus,* the structure responsible for the mechanical difficulty is the large, thick walled penis papilla although the heavy, annular intrinsic muscle cannot be disregarded in this matter. Though nearly eighty specimens were examined, no aphallate *stramineus* was found. It is possible that the somewhat smaller genital structures plus the reduced intrinsic muscle provide the minimum of impediment. Apophallation probably occurs, but it is apparently very rare.

Apophallation has not been shown elsewhere in this family and this is probably explainable by the fact that nowhere in this family do the genital structures attain such a relatively huge size. As exemplified in the titanic mesozoic reptilians and the carboniferous insects, gigantism is one form of specialization which frequently predisposes extinction. It is the writer's opinion that this genus similarly represents an evolutionary "blind alley" in which hypertrophy of the genital structures, especially the penis, has proceeded to the maximum — so much so, in fact, that individuals frequently must commit auto-amputation to pay for their efforts to maintain the species! Quite another evolutionary line is the one which gave rise to the aphallate Arioninae. Here, the genital evolution proceeded in just the opposite direction for the primitively small penis, which is found in *Anadenus*, the most primitive genus of this subfamily, atrophied completely leaving but an epiphallus or ejaculatory duct between the vas deferens and atrium. This line has been much more successful having given rise to several distinct genera whereas *Ariolimax* is the sole genus in its line.

Pilsbry, in his masterful work on the phylogeny of this family (1898b), minimized the importance of the penial structure as an index to phylogenetic relationships with this statement regarding degeneration of the penis, "This modification, it is demonstrated, occurred independently in several genera of the family." He was misled by his own genus *Aphallarion*, for all aphallate genera are rather closely related and nicely limited to the Arioninae. His misinterpretations of the penial structures of *Ariolimax* further hid from his view the real phylogenetic significance of these structures.

In light of this new evidence, Pilsbry's phylogenetic tree (*l. c.*, p. 102) would be somewhat altered as here shown. The relationships are more clear if a *hypothetical primitive penate stock* is introduced into the picture. This presumably evolved from the Binneyinae and would be characterized by the following: small size, hollow tail containing viscera, shell completely buried in mantle, caudal slime gland a slit, retractor muscles of tentacles and pharynx convergent, retentor muscle present, no genital appendiculum, a small penis papilla contained within a large penis sheath, and a terminal retractor of the penis. It can be seen that *Hesperarion* stands very close to this hypothetical stock differing only in having an appendiculum, which has evolved sporadically and apparently rather easily throughout the Pulmonata, and lacking a retentor muscle. This latter, as explained in the discussion of the genus, probably has no particular function in the slugs and for this reason there would be little premium put on retaining it; its loss then probably has been irregular in the family and therefore not greatly significant. *Ariolimax* evolved from this stock with a great increase in size, a development of caudal slime gland plug, and a considerable hypertrophy of the genital structures and especially the penis papilla which became wholly evaginated in some species. The convergent retractor muscles place *Hesperarion* and *Ariolimax* together in Ariolimacinae but they are not placed on the same stem as there are greater differences between them than between either of them and the hypothetical stock.

The Arioninae, with the divergent retractor muscles, branched off the primitive stock as a third and more successful evolutionary line. After the retentor was early independently lost and after the stock which gave rise to the genus *Anadenus* and perhaps other genera now extinct were evolved, the penis completely atrophied and this stock, in turn, gave rise to the aphallate genera of this subfamily.



Origin and Distribution

With a complete absence of any dependable fossil records, any hint as to the probable origin and distribution of the genus *Ariolimax* would have to be sought in the present distribution of its species and in the distribution and affinities of the other genera in the family Arionidae. Such limitations obviously restrict a discussion of this subject to mere speculation; nonetheless, such speculation is not wholly without value. In 1898, Pilsbry presented a hypothesis on the phylogeny of the family which seems so reasonable, in view of the meager available data, that it has gained wide acceptance. But with a better understanding of the genus *Ariolimax* and with the introduction of the significant study of penial homology, the origin and distribution of the genera of Arionidae would seem to be slightly different from that proposed by Pilsbry, though this new information actually lends further support to the main aspects of his hyopthesis. With the incorporation of these new data and some speculative elaborations, the origin and distribution of the Arionidae and *Ariolimax* in particular might be supposed to have taken place in the following manner.

The Arionidae originated probably in the Mid- or Late Tertiary period

in North American latitudes far north of where they are now most commonly found. Presumably by the beginning of the Pliocene, the three following ancestral stocks had branched off the Primitive Penate Stock (*q. v.*): one which gave rise to *Hesperarion* (and perhaps *Zacoleus*) which retained the small penis and the convergent free retractor muscles but had lost the retentor; one which gave rise to *Ariolimax* which retained the convergent free retractor muscles and the retentor but had evolved a very large penis; and one which gave rise to the Arioninae which retained the small penis but had lost the retentor and had evolved divergent free retractor muscles. This latter ancestral stock soon broke into two groups, one retaining the small penis and the other losing it. During this period, or perhaps in the Pleistocene, all of these groups underwent considerable distribution. The two arionine stocks passed independently westward presumably over a north Pacific land bridge into Asia; the aphallate stock, however, had already evolved *Prophysaon* (and perhaps *Anadenulus*) before this. The other groups and their progenitors, on the other hand, spread to the south on the North American continent.

With the advent of the glacial periods of the Pleistocene, there was a great southward migration on both continents with probably some groups becoming extinct. With continued intermittent periods of glaciation, further migration in Asia was limited to the temperate regions still further west. The more successful aphallate arionines migrated to Europe where they are represented by *Arion* and *Geomalacus*. (*Oopelta* also may have been derived from this stock.) No representatives have yet been found in Asia. The phallate stock remained in southern Asia and is known today only by the genus *Anadenus*. According to Pilsbry, the American and European arionines underwent an independent degeneration of the penis. This he offered to explain the presence of the penis in the Asiatic *Anadenus* and the absence of it in the American *Prophysaon* and *Aphallarion*. An American genesis of phallate and aphallate arionine stocks with subsequent independent migration to Asia seems just as logical and probably more tenable.

In *Ariolimax*, the distribution of *stramineus* is significant for its apparent endemicity* on the Santa Barbara Islands indicates that this subspecies migrated to this territory in Pleistocene times from continental populations. Moreover, the identical nature of present-day specimens on these islands and on the continent in the same latitudes, is indicative of a rather high degree of stability. The abrupt northern limit of this subspecies in the Salinas Valley district suggests that it became distinct from *columbianus* and attained its original southern distribution in the early Pliocene prior to the Pliocene marine inundation of the Salinas Valley. Santa Rosa and Santa Cruz Islands are the only two on which *stramineus* has been found; the smaller and more

* It must be borne in mind that there remains the possibility that these slugs were taken onto the islands by early French settlers; or what is less likely, they may have drifted from the continent on plant debris. The presence of Pleistocene elephant remains on the islands strongly supports the existence of a Pleistocene land connection along which these slugs could have migrated.

barren Anacapa and San Miguel Islands have not been able to maintain populations of this subspecies. Kanakoff (*in litt.*) reports that he had not been able to find it on Santa Catalina Island which is considerably to the south and has a quite different geological history. Gregg (*in litt.*), Berry (1909), and Baily (*in litt.*) have not been able to find it in Los Angeles, San Bernardino, and San Diego counties, respectively, though it is conceivable that it might have migrated along the coastal ranges to the latter county. There has been found but a single unauthentic record (Orcutt) from San Diego. Cooper (1892) did not report it from the Farallon Islands.

Typical maculate *columbianus* is found directly north of the Salinas Valley within a relatively few miles of typical *stramineus*. From here and from the western slopes of the Sierra Nevada in Tuolumne County, this species extends north into southeastern Alaska. The present distribution is not in itself significant, except for its abrupt southern, coastal limits, as it represents a secondary northern incursion which took place contemporaneously with the recession of the last glacial ice sheet. It is for this reason that a detailed list of northern locality records has not been compiled in this paper. Like many other species in the humid regions of the north, melanism was extensively developed.

The restriction of the *californicus-brachyphallus-dolichophallus* group to rather limited ranges in the region between San Francisco Peninsula and Salinas Valley reflects a more recent evolution, as does the comparative study of the genitalia, than the widespread *columbianus* group. Its origin might conceivably have been in this region during the very unstable Pleistocene with subsequent distribution being limited by San Francisco Bay, Santa Clara Valley, Salinas Valley, Monterey Bay, and the Pacific Ocean. The more primitive *columbianus*, however, got into this district before all these barriers came into effect for it is found in San Francisco and just north of Salinas. *Dolichophallus* has a greater range than the less primitive *californicus* or its subspecies though it strangely does not seem to have invaded territory of the latter. Its abrupt southern limits in the Salinas Valley district is likewise significant.

REFERENCES

ALLEN, JOHN A. 1916—Edibility of Polygyra and Ariolimax. Nautilus **29**:143.

BABOR, J. F. 1900—Mittheilungen über Nacktschnecken in der Sammlung des k. k. naturhistorischen Hofmuseums. Annal. k.k. Naturhist. Hofmuseums **15**:95-100.

BERRY, S. S. 1909—The known Mollusca of San Bernardino County, California. Nautilus **23**:73-79.

BINNEY, AMOS. 1851—The terrestrial air-breathing mollusks of the United States.... Boston, Charles C. Little and James Brown. 3 vols.

BINNEY, W. G. 1858—Notes on American land shells, no. 4. Proc. Acad. Nat. Sci. Phila., **10**:197-211.

———1859—The terrestrial air-breathing mollusks of the United States.... vol. iv. Boston Journ. Nat. Hist. **7**:viii + 207, pls. lxxv-lxxx.

———1860—Check list of the shells of North America. Smiths. Misc. Coll., 1860.

———1863—Synopsis of the air-breathing mollusks of North America. (Distrib. in form of proof sheets only as part of Smithsonian collections, Dec. 9, 1863, 12 pp.)

———1864—Bibliography of North American conchology previous to the year 1860. Part I, American authors. Smiths. Misc. Coll. **5**:vii + 650.

———1865—Description of genus Ariolimax, Mörch. Amer. Journ. Conch. **1**(2):48, pl. 6, f. 11-13.

———1869—Bibliography of North American conchology previous to the year 1860. Part II, Foreign authors. Smiths. Misc. Coll. **9**:v + 306.

———1873—Catalogue of the terrestrial air-breathing mollusks.... Bull. M. C. Z. Harvard **3**(9):191-220, map.

———1874—On the anatomy and lingual dentition of Ariolimax and other Pulmonata. Proc. Acad. Nat. Sci. Phila. **26**:33-63, pls. ii-xi.

———1876—On the lingual dentition, jaw, and genitalia of Carelia, Onchidella, and other Pulmonata. Proc. Acad. Nat. Sci. Phila. **28**:183-192.

———1878—The terrestrial air-breathing mollusks of the United States.... vol. v. Bull. M. C. Z. Harvard **4**:1-449, pls. i-xvi (and pls. i-lxxiv of vol. iii).

———1879—On the jaw and lingual dentition of certain terrestrial mollusks. Bull. M. C. Z. Harvard **5**:331-368, pls. i, ii.

———1883—A supplement to the fifth volume of the terrestrial air-breathing mollusks of the United States and adjacent territories. Bull. M. C. Z. Harvard **11**: 135-166, pls. i-iv.

———1885—Manual of American land shells. U.S.N.M. Bull. **28**:528 pp., 514 figs. (Catalogue of Binney Collection, pp. 473-499.)

———1886—A second supplement to the fifth volume of the terrestrial air-breathing mollusks of the United States and adjacent territories. Bull. M. C. Z. Harvard **13**:2-48, pls. i-iii.

———1890—Third supplement to the fifth volume of the terrestrial air breathing mollusks of the United States and adjacent territories. Bull. M. C. Z. Harvard **19**:183-226, pls. i-xi.

——— AND THOMAS BLAND. 1869—Land and fresh water shells of North America. Pt. I. Pulmonata Geophila. Smiths. Misc. Coll. **8**(194):xii + 316.

BLAND, THOMAS AND W. G. BINNEY. 1873—On the lingual dentition and jaw of certain terrestrial Pulmonata from the United States, with remarks on their systematic value. Proc. Acad. Nat. Sci. Phila. **25**:240-256.

———1874—On Prophysaon, a new pulmonate mollusk, on Ariolimax, on Helix lychnuchus, and other species. Annals N. Y. Lyc. Nat. Hist. **10**:293-311, pls. xiii, xiv.

CARPENTER, PHILIP P. 1857—Report on the present state of our knowledge with regard to the Mollusca of the West Coast of North America. Rept. Br. Assoc. Adv. Sci. 1856, **26**:159-368. (Also separately printed: London, Taylor and Francis, 1857.)

———1864—Supplementary report on the present state of our knowledge with regard to the Mollusca of the West Coast of North America. Rept. Br. Assoc. Adv. Sci. 1863, **33**:517-686. (Also in Smiths. Misc. Coll. **10**(252):xii + 172 incl. index to both vols.)

COCKERELL, T. D. A. 1890—Notes on slugs, chiefly in the collection at the British Museum. Ann. Mag. Nat. Hist., 6 ser., **6**:277-288; 380-390. **7**:97-107; 328-341.

———1891—The slugs of British Columbia. Nautilus **5**:30-32.

———1893—A check list of the slugs. With appendix and notes by Walter E. Collinge. Conchologist **2**:168-176; 185-232.

———1897—Notes on slugs. Nautilus **11**:75-79.

COOPER, WILLIAM. 1860—Report upon the Mollusca collected on the survey. Zoological report, no. 6. Reports of explorations and surveys, to ascertain the most practicable and economical route for a railroad from the Mississippi River to the Pacific Ocean. 1853-5. **12**(2):369-386. [With notes by J. G. Cooper.]

COOPER, J. G. 1867—Geographical catalogue of the Mollusca found west of the Rocky Mountains, between latitudes 33° and 49° North. Geological Survey of California. San Francisco, Towne & Bacon, Printers, 40 pp.

———1870—Notes on Mollusca of Monterey Bay, California. Amer. Journ. Conch. **6**:42-70.

———1872—On new Californian Pulmonata, etc. Proc. Acad. Nat. Sci. Phila. **24**:143-154.

———1873—On shells of the West slope of North America. Proc. Cal. Acad. Sci. **4**:150-154, pl. i.

———1876—On shells of the west slope of North America no. III. Proc. Cal. Acad. Sci. **6**:14-27.

———1879—Notes on some land-shells of the Pacific slope. Proc. Amer. Phil. Soc. **18**:282-288.

———1886—On fossil and sub-fossil land shells of the United States, with notes on living species. Cal. Acad. Sci. Bull. **1**:235-255.

———1887—West Coast Pulmonata; fossil and living. Cal. Acad. Sci. Bull. **2**:355-376, map; 497-514.

———1889—West Coast Pulmonata; fossil and living. Proc. Cal. Acad. Sci., 2 ser., **1**:11-24.

———1890—Additional notes and descriptions of new species. Proc. Cal. Acad. Sci., 2 ser., **3**:70-91, 1 pl.

———1892—On the natural history of the Farallon Islands. Mollusca. Zoë **3**:151-153.

———1894—Catalogue of West North American and many foreign shells with their geographical ranges. For labels, exchange, and check lists. Sacramento, Printed for the State Mining Bureau, April, 1894. [no pagination]

CRAIG, ELBERTA L. 1927—Some mollusks and other invertebrates from the northwest. Univ. Colo. Stud. **16**:63-74.

DALL, WILLIAM H. 1905—Land and freshwater mollusks of Alaska and adjoining regions. Harriman Alaska Expedition **13**:1-171, pls. i, ii, 118 figs. in text. New York, Doubleday Page & Company.

GOULD, A. A. 1851—See Binney, Amos.

———1852—Mollusca and shells. United States Exploring Expedition.... under the command of Capt. Charles Wilkes. **12**:xv + 510, 52 pls.

GRATACAP, L. P. 1901—Catalogue of the Binney and Bland collection of terrestrial air-breathing mollusks of the United States and territories in the American Museum of Natural History, with enumeration of types and figured specimens, and supplementary notes. Bull. Amer. Mus. Nat. Hist. **14**:335-461, pls. xli-xlvi, 6 maps.

GRATELOUP, J. P. S. DE. 1855—Distribution géographique de la famille des Limaciens. Bordeaux, Th. Lafargue. iv + 33 pp.

HANHAM, A. W. 1914—Notes on mollusks from British Columbia. Nautilus **28**:87-88.

HEATH, HAROLD. 1916—The conjugation of Ariolimax californicus. Nautilus **30**:22-24.

HEMPHILL, HENRY. 1891—Ariolimary [*sic*] Columbianus var. straminea. Nautilus **4**:120.

HENDERSON, JUNIUS. 1927—Mollusk notes from the northwest. Nautilus **40**:75-78.

———1929—None-marine Mollusca of Oregon and Washington. Univ. Colo. Stud. **17**:47-190, 186 figs.

———1936—Supplement. *op. cit.* **23**:251-280.

HESS, P. 1926—Die Nacktschnecken der palaearktischen Region. Archiv f. Molluskenkunde, Abhandl. **2**:1-152, 2 pls.

HEYNEMANN, D. F. 1885—Die nackten Landpulmonaten des Erdbodens, Jahrb. Deutsche Malakozool. Gesell. **12**:236-330.

———1909—Die geographische Verbreitung der Nacktschnecken. Senckenberg. Naturfors. Gesell. Abhandl. **30**:1-92, 11 maps.

INGRAM, W. M. 1942—Food habits of Haplotrema minimum Ancey and habits of associated mollusks on the Mills College Campus. Nautilus **55**:98-102.

KEEP, JOSIAH AND JOSHUA L. BAILY, JR. 1935—West Coast shells. Stanford Univ. Press. 350 pp., 334 figs.

KEFERSTEIN, WILHELM. 1862-66—Der Weichthiere (Malacozoa). *In*.... Bronn, Die Klassen und Ordnungen des Thier-reichs.... Leipzig u. Heidelberg, C. F. Winter, **3**(2):523-1500, pls. xlv-cxxxvi, 136 figs. in text.

KÜKENTHAL, WILLY AND THILO KRUMBACH. 1926—Pulmonata—Lungenschnecken. *In their*.... Handbuch der Zoologie.... Berlin u. Leipzig, Walter De Gruyter & Co. **5**(2):116-155.

MARTENS, EDUARD VON. 1890-1901—Land and freshwater Mollusca. *In*.... Godman & Slavin, Biologia Centrali-Americana **38**:1-675, 44 pls.

MÖRCH, O. A. L. 1860—Beiträge zur Molluskenfauna Central-Amerika's. Malak. Blätter **6**:110.

ORCUTT, C. R. 1915—Molluscan world. vol. 1. West American Scientist **20**:62 + 208.

PILSBRY, H. A. 1889—Check-list of North American land shells. Proc. Acad. Nat. Sci. Phila. **41**:191-210.

———1898a—A classified catalogue of American land shells, with localities. Nautilus **11**:45-48, 59-60, 71-72, 83-84, 93-96, 105-108, 117-120, 127-132, 138-144. (Reprinted by Pilsbry and Johnson, C. W., with corrections and change of title as a separate publication, 35 pp. April, 1898.)

———1898b—Phylogeny of the genera of Arionidae. Proc. Malac. Soc. London **3**:94-104, pl. vii.

———1900—A new American slug. Nautilus **14**:71-72.

———1903—A new American genus of Arionidae. Proc. Acad. Nat. Sci. Phila. **55**:626-629, pl. xxviii.

——— AND E. G. VANATTA. 1896—Revision of the North American slugs: Ariolimax and Aphallarion. Proc. Acad. Nat. Sci. Phila. **48**:339-350, pls. xii-xiv.

———1898—Revision of the North American slugs: Binneya, Hemphillia, Hesperarion, Prophysaon and Anadenulus. Proc. Acad. Nat. Sci. Phila. **50**:219-261, pls. ix-xvi.

PRATT, H. S. 1935—A manual of the common invertebrate animals exclusive of the insects. Philadelphia, P. Blakiston's Son & Co., Inc. xviii + 854 pp.

RAYMOND, W. J. 1903—Writings of James G. Cooper, M.D., on conchology and palaeontology, with list of species described by him. Nautilus **17**:6-12.

SIMROTH, H. 1891a—Hesperarion, eine neue amerikanische Nacktschnecken-Gattung. Malak. Blätter, 2 ser., **11**:109-119, pl. i, f. 5-14.

———1891b—Die Nacktschnecken der portugiesisch-azorischen Fauna in ihrem Verhältniss zu denen der paläarktischen Region überhaupt. Nova Acta K. Leop.-Carol. Acad. Nat. Cur. **56**:203-424, 8 col. pls.

——— AND H. HOFFMANN. 1908-1928—Pulmonata. *In*. . . . H. G. Bronns Klassen und Ordnungnen des Tier-reichs. **3**:2:2:xvi + 1354, 44 pls. part col., 561 figs. in text.

TAYLOR, G. W. 1891—Land shells of Vancouver Island. Nautilus **5**:91-92.

THIELE, JOHANNES. 1931—Handbuch der systematischen Weichtierkunde. **2**:377-778. Jena, Gustav Fischer.

TRYON, GEORGE W., JR. 1866-68—Monograph of the terrestrial Mollusca of the United States. Amer. Journ. Conch. **2**:218-277, 306-327; **3**:34-80, 155-181, 298-324; **4**:5-19, 18 pls.

———1882-84—Structural and systematic conchology; an introduction to the study of the Mollusca. Philadelphia, pub. by the author, 3 vols., 140 pls.

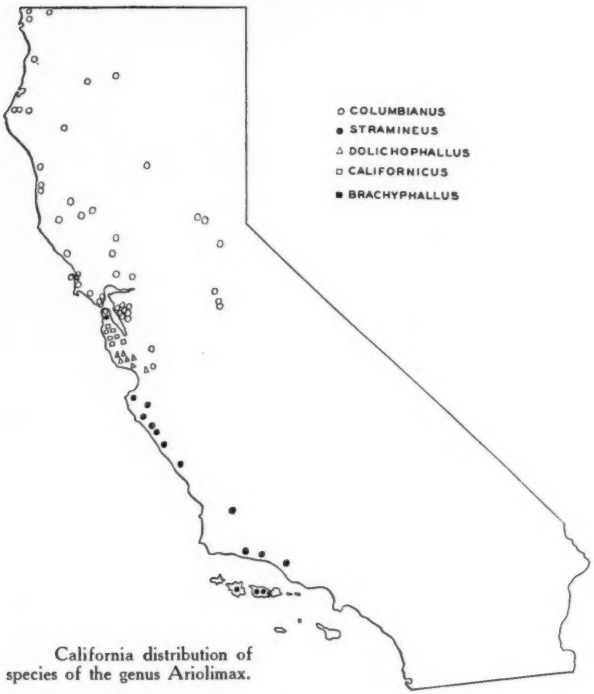
———1885—Manual of chonchology; structural and systematic. Acad. Nat. Sci. Phila., 2 ser., **1**:1-364, 60 pls.

WASTE, R. J. 1937—The land slugs of California. Berkeley, Univ. Calif. M. A. thesis. [not pub.]

WETHERBY, A. G. 1880—Some notes on American land shells. Cincinnati Soc. Nat. Hist. Journ. **3**:33-40.

WOOD, W. M. AND W. J. RAYMOND. 1891—Mollusks of San Francisco County. Nautilus **5**:54-58.

YATES, L. G. 1890—The Mollusca of Santa Barbara County, California. Bull. Santa Barbara Soc. Nat. Hist. **1**:37-45.



California distribution of species of the genus Ariolimax.

EXPLANATION OF PLATES

Ap—apical penis; AT—atrium; AV—apical vas deferens; B—bulb; BP—basal penis; BV—basal vas deferens; CT—connective tissue; E—ejaculatory duct; EM—extrinsic muscle of vagina; FO—free oviduct; G—glans; IM—intrinsic muscle of vagina; M—muscle mass of sheath; O—genital orifice; OS—ovosperm duct; PP—penis papilla; PS—penis sheath; RMP—retractor muscle of penis; S—spermatheca; V—vagina.

PLATE 1

Fig. 1, *Ariolimax californicus* Cooper, basal genital structures. Fig. 2, *Ariolimax californicus brachyphallus* n. subsp., basal genital structures. Fig. 3, *Ariolimax columbianus stramineus* Hemphill, basal genital structures. Fig. 4, *Ariolimax dolichophallus* n. sp., basal genital structures.

PLATE 2

Fig. 5, *Ariolimax columbianus* (Gould), basal genital structures. Fig. 6, *Hesperarion niger* (Cooper), penis with sheath cut open to show internal papilla. Fig. 7, *Hesperarion niger* (Cooper), longitudinal section through apical penis and vas deferens. Fig. 8, *Ariolimax columbianus* (Gould), longitudinal section through penis and vas deferens. Fig. 9, *Ariolimax californicus* Cooper, penial apex completely invaginated. Fig. 10, *Ariolimax californicus* Cooper, penial apex beginning to evaginate. Fig. 11, *Ariolimax californicus* Cooper, further evagination of penial apex. Fig. 12, *Ariolimax californicus* Cooper, penis completely evaginated.

PLATE 1

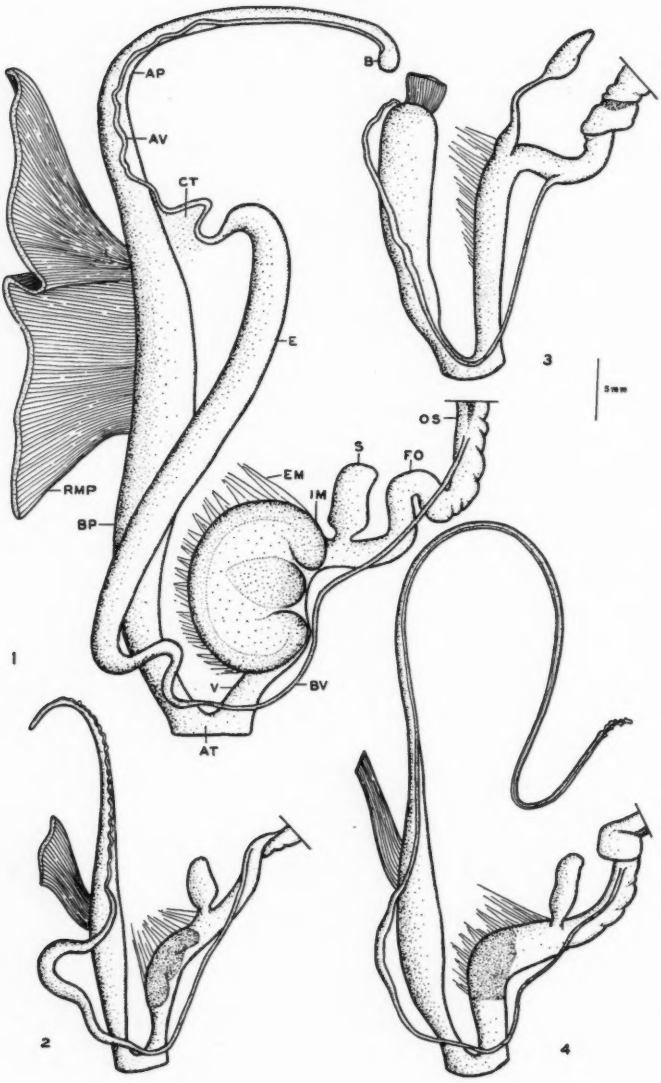


PLATE 2

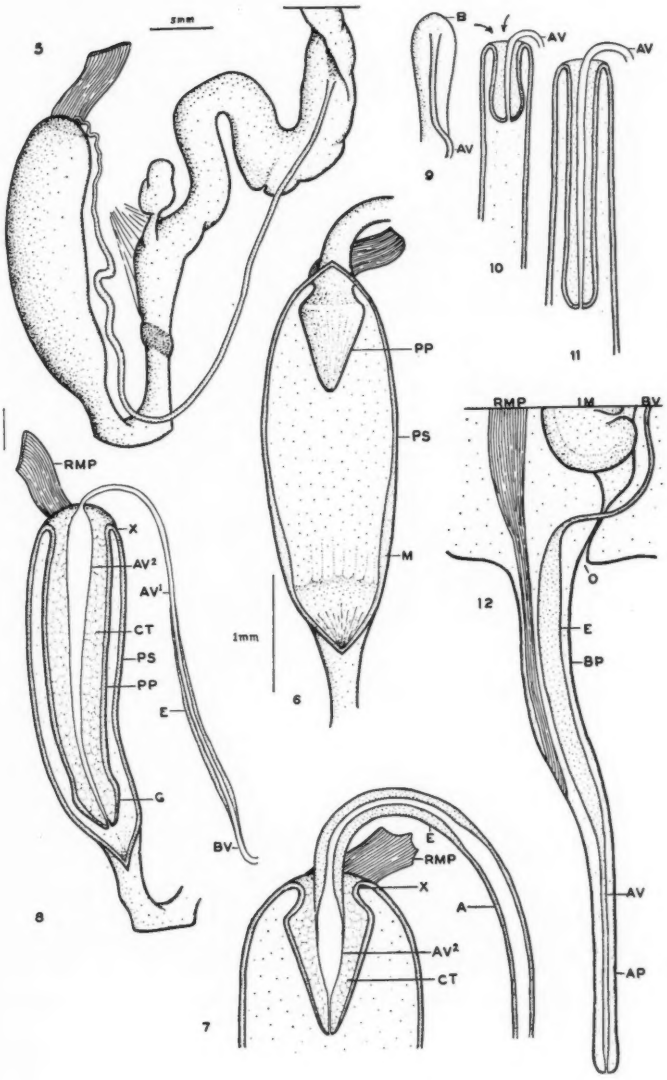
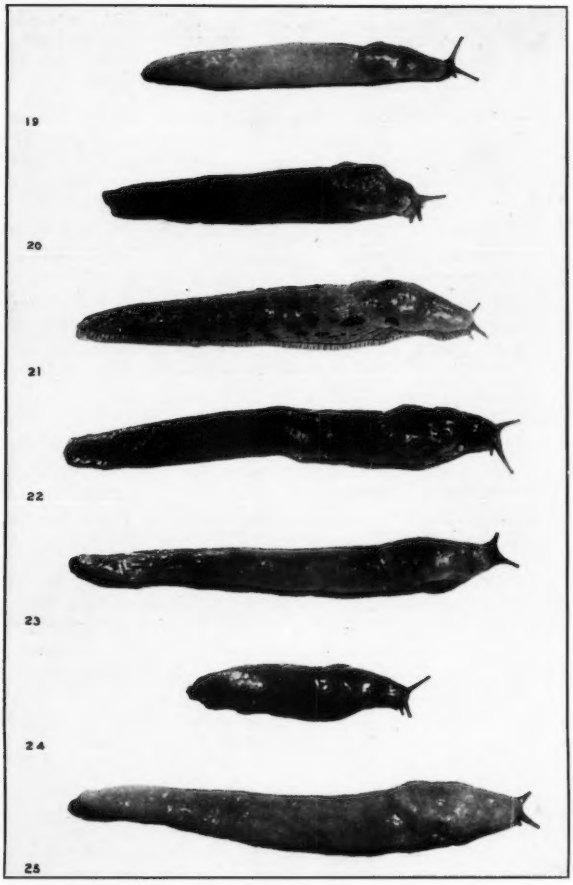

5
2mm
9
B
AV
10
AV
11
AV
PP
PS
M
6
1mm
RMP
X
AV²
AV¹
CT
PS
PP
E
G
BV
8
RMP
IM
BV
O
12
E
BP
AV
AP
E
RMP
X
A
AV²
CT
7

PLATE 3

Fig. 13, *Ariolimax columbianus stramineus* Hemphill, genitalia. Fig. 14, *Ariolimax columbianus* (Gould), genitalia. Fig. 15, *Ariolimax californicus* Cooper, genitalia. Fig. 16, *Ariolimax dolichophallus* n. sp., genitalia. Fig. 17, *Ariolimax californicus brachyphallus* n. subsp., genitalia. Fig. 18, *Ariolimax dolichophallus* n. sp., genitalia of aphallate specimen.

PLATE 4



All figures about 3/8 natural size. Fig. 19, *Ariolimax columbianus stramineus* Hemphill. Big Sur State Park, California. Fig. 20, *Ariolimax columbianus* (Gould), Henry, California. Fig. 21, *Ariolimax columbianus* (Gould), Redwood Hwy. Quar. Stn., California. Fig. 22, *Ariolimax columbianus* (Gould), Inverness, California. Fig. 23, *Ariolimax dolichophallus* n. sp., Saratoga, California. Fig. 24, *Ariolimax californicus brachyphallus* n. subsp., Mt. Davidson, California. Fig. 25, *Ariolimax californicus* Cooper, Lake San Andreas, California.

Records and Descriptions of North American Crane-Flies (Diptera)[1]

Part IV. Tipuloidea of the Yellowstone National Park

Charles P. Alexander

General Account

The Yellowstone National Park lies principally in northwestern Wyoming, with slight encroachments upon Idaho and Montana, forming a roughly rectangular area having a total of 3472 square miles, or approximately 2,222,000 acres. The central portion of the park is essentially an elevated volcanic plateau with an average altitude of between 7,000 and 8,000 feet, with several peaks, including Mount Washburn, exceeding 10,000 feet. Approximately four-fifths of the total park area is forested, almost entirely by coniferous tree types, particularly pines. About three-fourths of the tree population consists of lodgepole pine, *Pinus murrayana* Balf., the remainder chiefly of whitebark pine, *Pinus albicaulis* Engelm., alpine fir, *Abies lasiocarpa* (Hook.) Nutt., and Engelmann spruce, *Picea engelmannii* (Parry) Engelm., at the higher levels; and limber pine, *Pinus flexilis* James, Colorado Douglas fir, *Pseudotsuga glauca* Mayr, and Rocky Mountain red cedar, *Juniperus scopulorum* Sarg., at somewhat lower elevations. The most common deciduous tree in the park is the quaking aspen, *Populus tremuloides* Michx.

The continental divide extends from the Montana-Idaho border at the west of the park diagonally and irregularly southeastward to near the southeastern corner of the area, passing just to the south of the Lone Star geyser, near Old Faithful. Thus virtually all of the species of Tipuloidea recorded herein were taken to the east of the divide, the only exceptions being such materials as were taken at Lewis Lake and southward along the Lewis River. The peculiar system of drainage in the park and adjacent regions is well expressed by Disterdick (in Climate and Man, p. 1209; 1941):

> The drainage of Wyoming is remarkable in that its waters flow in practically every direction, and tributaries of three great river systems have their sources in a rather limited area in the northwest part of the State. The Green River, a tributary of the Colorado, has its source in the northern part of Sublette County, and flows into the Gulf of California. The Snake River has its source in the area adjacent to the southern part of Yellowstone Park and the western slopes of the Wind River and Gros Ventre mountain ranges; it is a tributary of the Columbia. The Missouri and the Yellowstone

1 The preceding part under this general title was published in the American Midland Naturalist **29**:147-179; 1943.

References in the text refer to the bibliography at the conclusion of the general account.

In all cases in this report where no collector is given, the specimens were secured by the author. M. M. Alexander—Mrs. Charles P. Alexander.

Rivers have their sources in Yellowstone Park, and the Big Horn, a tributary of the Yellowstone, has its source on the east slope of the Wind River and Absaroka mountain ranges; all these streams are a part of the Mississippi River system.

The main scenic attractions of the park, including the marvellous series of geysers, hot springs, mud volcanoes, and paintpots; the Grand Canyon of the Yellowstone River with its magnificent waterfalls; Yellowstone and other major lakes; and the preserves of mammals and birds, all are known so well that they are not further mentioned in the present report. In addition to the larger lakes of the park, there are rather numerous smaller lakes and ponds throughout the area. Sphagnum bogs, with sundews and other characteristic oxylophytic plants occur but do not seem to be common. The lakes and rivers are fed by smaller streams and brooks, many of the latter winding through the lodgepole pine forests and out into open meadows that support a rich and varied herbaceous flora. Most of the crane-flies discussed in the present paper were taken by sweeping the vegetation along the smaller streams such as described.

In such a varied ecological habitat one would expect to find a rich crane-fly fauna and this has proved to be the case. It is surprising that up to the present moment there is scarcely a single published reference to the crane-flies of the Yellowstone, and, further, that there have been only a very few specimens of these flies preserved in the major museums and public collections. Small series that have generously been given to me include materials taken by Dr. M. D. Leonard in Gibbon Canyon, July 1929; and others taken by Professor G. F. Knowlton and Mr. H. F. Thornley in September 1941. The chief collections available for the present study were those made by the author and Mrs. Alexander in 1934, 1941 and 1942, including some thousands of specimens representing approximately 80 species. Virtually all of this material was taken between the dates of June 21 and July 14, representing the early season fauna, with the result that the late season species are still poorly known. It is probable, however, that there does not exist such a striking difference between the spring and fall species as is found in northeastern North America, for example, where the crane-flies occurring in June are almost entirely different from those species on the wing in late August and September.

Life Zones.—Of the seven life zones or faunal areas commonly differentiated in North America, four are found within the park limits, as follows:

Transition (Foothills). Occurs in limited areas in the low-lying valleys up to approximately 7,500 feet on the southwestern slopes, 6,500 on the colder northeastern slopes.

Canadian (Montane). This covers most of the park between 7,500 and 9,000 feet on the southwestern slopes, and 6,500 and 8,000 feet on the northeastern ones. It includes the general plateau level of the park, with the chief forested areas, all the major lakes, the three great geyser basins, and the Grand Canyon of the Yellowstone. Most of the crane-fly collecting done by the writer was in this zone.

Hudsonian (Subalpine). Restricted to narrow belts of scrubby tree growth

immediately below timberline on the higher peaks and ridges. It is rarely more than 1,000 feet in vertical extent, occurring between 9,000 and 10,000 feet on the warmer southwestern exposures, and between 8,000 and 9,000 feet on the cold northeastern slopes.

Arctic-Alpine (Alpine). Occurs above extreme timberline on the highest peaks and ridges, above 10,000 feet on warm sunny exposures, above 9,000 feet on cold shaded slopes.

(References to life zones of Yellowstone: Bailey, 1930: 9-15; Cary, 1917; Skinner, 1925. The Bailey and Cary references are accompanied by colored life zone maps and are particularly useful.)

By Fenneman's classification (1931) of the United States into physical divisions, the Yellowstone falls chiefly in the Middle Rocky Mountain Province, the extreme northwestern section in the Northern Rocky Mountain Province, both of the Rocky Mountain System. By Mulford's division of the United States into plant-growth regions (Van Dersal, 1938: 16-27, map), the area falls in Region 12, the Northern Rocky Mountains.

Collecting Stations.—In 1941, the writer and Mrs. Alexander, with the co-operation of Mr. and Mrs. Walter H. Harrison, of Amherst, Massachusetts, established seven stations distributed throughout the park that were made the basis for special study of the Tipulidae. These collections were made between June 21st and 30th and represent the early spring fauna, particularly at the higher altitudes. In 1942, Mrs. Alexander and I again collected in the park but due to a serious foot injury incurred earlier, collecting was greatly hampered and the results were scarcely satisfactory. The 1942 series was taken between July 10th and 13th and it was anticipated that this slightly later date over the collections of the preceding year would show a marked change in the crane-fly fauna of the various stations. However, in 1941 the season was advanced whereas in 1942 conditions were notably retarded, with the result that virtually the same crane-fly species were on the wing on July 12, 1942, as on June 30, 1941. The seven base stations established in 1941 are as follows:

1. Sylvan Lake and vicinity, altitude 8,000 feet, June 21, 1941. Collections made in the lodgepole forests, here intermixed with fewer Engelmann spruce. Conditions definitely early spring, with large patches of snow persisting in the nearby woods and with extensive beds of snow lily, *Erythronium parviflorum* (Wats.) Good, in full flower near by. Collections made in a swale where small mountain streams had ramified and produced an extensive swampy area, with many signs of elk and mule deer. Labelled "Sylvan Lake"; in 1942, a further brief survey of the area was made on July 13th.

2. Canyon Camp, altitude 7,800 feet; and about the Upper and Lower Falls of the Yellowstone River, as low as 7,500 feet; June 20 and 22; not duplicated in 1942. Forest almost entirely of lodgepole pine.

3. Tower Falls, collections made in wet swales along Tower Creek, above the falls, altitude 6,500 feet, June 23, 1941; further collections in the great gorge at the foot of Tower Falls, altitude about 6,200 feet, June 23, 25 and

26, 1941; not duplicated in 1942. This latter station is one of unusual interest although rather difficult to collect. Talus slopes at the foot of the falls mount the cliffs to a height of 100 feet or more, densely covered with herbaceous vegetation, including many grasses, *Heracleum lanatum* Michx., *Ranunculus* spp., and others. Numerous springs and small streamlets flow down these talus slopes where this is constantly in the spray of the falls, at this season a distance of some 200 to 250 feet from the base. Labelled "Tower Falls.'

4. Northeast Entrance; near Silver Gate, Montana; just inside the park boundaries but in Montana; altitude 7,200 feet; collections made June 24 and 26, 1941, chiefly along small mountain streams flowing down the mountain sides into Soda Butte Creek. Above the highway these streams are very steep and rapid-flowing; near the major creek they flow through wet meadows, providing fine collecting; not duplicated in 1942. Station within one mile of park boundary, near Amphitheatre and Abiathar Mountains; forest cover chiefly Engelmann spruce and alpine fir, with some Siberian juniper, *Juniperus communis montana* Ait. Floor plants include *Smilacina stellata* (L.) Desf.; *Linnaea borealis americana* Forbes, great beds, still in bud; *Thalictrum occidentale* Gray, and many others. Labelled "Northeast Entrance."

5. Obsidian Creek; some 300 yards north of Obsidian Cliff and directly beneath the northward extension of the same; altitude 7,300 feet; June 27, 1941; repeated July 11, 1942. Stream banks shaded with Engelmann spruce, alpine fir and some Siberian cedar; herbage consisting of dense growth of *Equisetum arvense* L., *Smilacina stellata; Aquilegia flavescens* Wats.; *Thalictrum occidentale,* and abundant reeds and rushes. Labelled "Obsidian Creek."

6. Elk Park, near Gibbon Meadow, altitude 7,000 feet; June 28, 1941; repeated July 11, 1942. Along trail to the Artists Paintpots from Gibbon Meadows. Collecting done along a small stream and in the adjacent wet areas, in a sparse open forest of lodgepole pine. The extensive wet flats chiefly covered with sedges and similar growth but with numerous large areas of *Pedicularis groenlandica* Retz., just coming into flower; less abundant *Limnorchis borealis* (Cham.) Rydb., and a yellow *Castilleja,* both in full flower; much *Smilacina stellata.* Along the actual stream, in very wet spots, abundant *Triglochin palustris* L. and *Mimulus Langsdorfii* Sims., the latter in full flower and very conspicuous. In places, young plants of *Heracleum lanatum;* on the higher knolls about the bases of the pines, beds of *Cornus canadensis* L., still chiefly in bud. Labelled "Elk Park."

7. Emerald Pool, Black Sand Geyser Basin; altitude 7,275 feet, June 29 and 30, 1941; repeated July 10 and 12, 1942. Remarkably fine collecting along a small brook flowing into Iron Creek, a branch of the Firehole River; near the Emerald Pool and only about two miles from Old Faithful Geyser. The small stream winds through an open woodland of lodgepole pine, with a rich vegetation of shrubs and herbs, including an unusually abundant and fine display of *Ledum glandulosum* Nutt., in full bloom. Other plants from which Tipulidae were swept included *Triglochin palustris, Camassia esculenta* Lindl., *Eriophorum ocreatum* A. Nels., *Limnorchis borealis, Thalictrum occidentale, Actaea arguta* Nutt., *Geranium Richardsonii* F. & M., *Veronica ameri-*

cana Schwein., in stream, *Mimulus Langsdorfii, Pedicularis groenlandica,* a red species of *Castilleja, Cicuta occidentalis* Greene, *Heracleum lanatum, Senecio serra* Hook., and others. The actual stream was almost choked with *Batrachium flaccidum* (Pers.) Rupe., and with abundant surface growth of *Lemna trisulca* L. In the more boggy areas, *Eriophorum* and abundant *Drosera longifolia* L. The small brook has many springs and lateral runlets that spread out over an extensive area and provide rich Tipulid collecting. Some further materials were taken by following a small creek up the mountainside to an altitude of about 7,400 feet. All collecting was done within 200 yards of Emerald Pool, south and west. On July 12, 1942, while collecting all afternoon, there were numerous elk watching from a short distance away. This station proved to be the richest and most interesting of any of those investigated within the park limits and well deserves still further study. Labelled "Emerald Pool."

Bear Tooth Mountains. Although lying just outside the park limits, along the Wyoming-Montana border to the northeast of the area, it is deemed advisable to include some discussion of the Tipulidae of the station since it adds materially to our knowledge of the high-altitude species of the north-central Rocky Mountains. Our party visited the station on June 24, 1941, driving over the beautifully graded high mountain road between Silver Gate, near the northeast park entrance, almost to Red Lodge, Montana. The road follows the crest of the Bear Tooth Range, winding between numerous alpine tarns and great snow masses (at this date); in two places the road reaches altitudes of 10,924 and 10,942 feet, respectively. At the time of our visit conditions were still far too early for any crane-flies but in August 1941 and again in 1942, representative collections at these high altitudes were made by our friends, Mr. and Mrs. John L. Sperry, of Riverside, California. Such specimens were taken chiefly at Quad Creek, 10,000-10,500 feet, for the most part in open mountain meadows where they were flying among and alighting upon the stunted alpine willows or flying among the dried-up grass on the mountainside. A discussion of these crane-flies, representing the highest Hudsonian or low Arctic-Alpine zones, will be found under *Tipula* (*Oreomyza*) *neptun* Dietz, *T.* (*Lunatipula*) *sperryana* Alexander, *T.* (*L.*) *dens-ursi* sp. nov., and *T.* (*L.*) *satyr* Alexander. Labelled "Bear Tooth Mountains."

I wish to express my deepest appreciation to Mrs. Alexander and to Mr. and Mrs. Harrison and Mr. and Mrs. Sperry, for their invaluable assistance in the collecting of Tipulid materials. I am further indebted to Dr. Harlow B. Mills, State Entomologist of Montana, former assistant Park Naturalist of the Yellowstone, and to Dr. C. Max Bauer, Park Naturalist, for advice concerning collecting localities and similar information.

REFERENCES

ANON. 1940—Yellowstone National Park, A Bibliography, pp. i-xxvi, 1-200 (compiled by H. H. Voth and C. P. Russell).—mimeographed, approximately 1,600 titles.

———1941—A bibliography of National Parks and Monuments west of the Mississippi

River, vol. 1: Yellowstone, pp. 1-200 (same as last but without the important preliminary "Concise history of scientists and scientific investigations," by Dr. Russell;) mimeographed. (These two very important references are quite indispensable to workers on the Yellowstone National Park; they were prepared by members of the National Park Service staff under the general direction of Dr. Dorr G. Yeager.)

(VARIOUS AUTHORS) 1941—Climate and Man. 1941 Yearbook of Agriculture. U. S. D. A., pp. 1-1248; Wyoming, pp. 1201-1210, 7 maps.

ALDRICH, JOHN M. 1928—The flies of the western mountains. Smithson. Inst., explorations and field work, **1927**:67-72, ill.

BAILEY, VERNON. 1930—Animal life of Yellowstone National Park, pp. 3-241, 70 figs. (C. C. Thomas Publ. Co., Springfield, Ill.); life zones, pp. 9-15, col. map showing zones of Yellowstone and Grand Tetons.

CARY, MERRITT. 1917—Life zone investigations in Wyoming. U. S. Biol. Surv., North Amer. Fauna **42**:1-95,. col. map, 14 pls., 17 figs.; map shows life zones of state, including Yellowstone.

FENNEMAN, NEVIN M. 1931—Physiography of western United States, pp. 1-534, 173 figs., 1 pocket map.

HAYNES, J. E. 1939—Haynes Guide, handbook of Yellowstone National Park, ed. **46**:7-194, maps, ills.

MCDOUGALL, W. B. AND HERMA G. BAGGLEY. 1936—Plants of the Yellowstone National Park, Nat. Park Serv., 160 pp., 6 pls., 115 figs.; discussion of types of vegetation, pp. 4-5.

MUTTKOWSKI, R. A. 1929—The ecology of trout streams in Yellowstone National Park. Roosevelt wild life annals **2**:155-240, ills., bibl.

PESMAN, M. WALTER. 1942—Meet the Natives—an easy way to recognize wild flowers, trees and shrubs of the central Rocky Mountain region, pp. 1-216, num. figs.; life zones, pp. 5-6, 11-14.

SKINNER, MILTON P. 1925—The birds of Yellowstone National Park. Roosevelt wild life bull. **3**:7-189, 2 maps, 4 col. pls., 47 figs., bibl.

VAN DERSAL, WILLIAM R. 1938—Native woody plants of the United States, their erosion-control and wildlife values. U.S.D.A. Misc. Publ. **303**:1-362, 44 pls., 2 pocket maps.

Systematic Account

PTYCHOPTERIDAE

Ptychoptera lenis Osten Sacken, 1877.—Obsidian Creek, 7,300 ft., June 27, 1941; Emerald Pool, 7,275 ft., June 29-30, 1941.

Ptychoptera pendula Alexander, 1937.—Swales near Northeast Entrance, 7,200 ft., June 24 and 26, 1941; Emerald Pool, 7,275 ft., June 29-30, 1941.

TIPULIDAE

TIPULINAE

Prionocera primoveris sp. nov.—Size small (wing, male, 11 mm. or less); mesonotal praescutum dark gray, with four ill-defined darker brownish

gray stripes that are narrowly and insensibly bordered by darker; pleura light gray; femora obscure brownish yellow, the tips rather narrowly brownish black, the amount subequal on all legs; wings with a weak brownish tinge; male hypopygium with the lateral tergal lobes very slender, yellow; caudal emargination produced into two flattened plates, the outer angles directed laterad into stout lobes, the mesal angles produced caudad into a slender glabrous arm; inner dististyle relatively narrow.

♂. Length, about 9-10 mm.; wing, 10.5-11 mm.; antenna, about 2.8-3.2 mm.

♀. Length, about 13 mm.; wing, 11.5-12 mm.

Rostrum entirely black; palpi black. Antenna relatively short, black throughout, the segments more or less pruinose; flagellar segments unusually short, subtriangular, producing only a weakly serrate effect; terminal (13th) segment abruptly reduced in thickness, as common in the genus. Head dark gray, the orbits narrowly light gray; anterior vertex wide, the eyes correspondingly small.

Pronotal scutum dark gray, the scutellum and pretergites abruptly light yellow. Mesonotal praescutum dark gray, with four ill-defined darker brownish gray stripes that are narrowly and insensibly bordered by darker; posterior sclerites of notum gray, the centers of the scutal lobes brown, not contrasting strongly against the ground; parascutella restrictedly yellowish on either side of scutellum, the remainder brown. Pleura light gray; dorsopleural membrane weakly infuscated. Halteres obscure yellow, the knob and outer face of stem dark brown. Legs with coxae light gray; trochanters yellow; femora obscure brownish yellow, the tips rather narrowly brownish black, the amount subequal on all legs and including the distal sixth to eighth of segment; tibiae dark brown, the tips still darker; tarsi black. Wings (Fig. 1) with a weak brownish

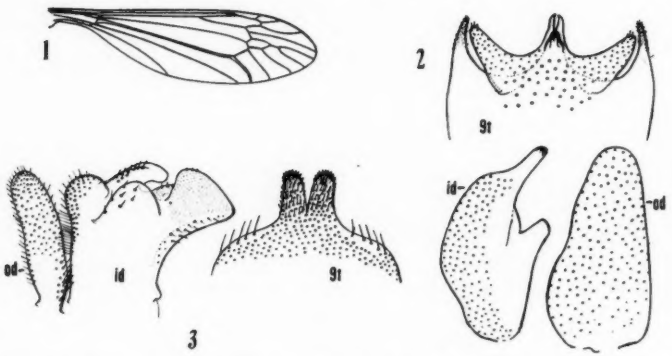


Fig. 1. *Prionocera primoveris* sp.n.; *venation*. Fig. 2. *Prionocera primoveris* sp.n., male hypopygium. Fig. 3. *Tipula (Yamatotipula) colteri* sp.n.; male hypopygium. (Symbols: *id*, inner dististyle; *od*, outer dististyle; *t*, 9th tergite.)

tinge, the stigma faintly darker, more or less bicolored, its proximal half paler than the outer portion; veins brown, *Sc* and prearcular veins yellow. Veins beyond cord virtually without trichia, there being none on R_{2+3}, R_{1+2}, R_3, or outer medial branches; a few scattered trichia on outer section of R_{4+5}. Venation: *Rs* relatively long, much exceeding R_3; cell M_4 long and narrow, gently widened outwardly.

Abdomen dark gray, the lateral tergal borders broadly buffy, the extreme caudal margins similarly pale; hypopygium dark, the outer dististyle obscure brownish yellow. Male hypopygium with the tergite (Fig. 2, *9t*) elongate, the lateral angles produced caudad into very slender yellow lobes that are provided with microscopic setulae; inside the outermost lobes with two flattened plates, the outer portions of which are directed laterad into stouter lobes, the mesal portion directed caudad into a slender glabrous lobe, on the median line almost touching its mate of the opposite side. Outer dististyle, *od*, relatively broad, more narrowed and obtuse at apex. Inner dististyle, *id*, relatively narrow as compared with other species.

Holotype, ♂, Sylvan Lake, Yellowstone, altitude 8,000 ft., June 21, 1941 (*C. P. Alexander*). *Allotype*, ♀, Twogwotee Pass, Grand Teton National Forest, Wyoming, 9,650 ft., July 9, 1942 (*C. P. Alexander*). *Paratopotype*, 1 ♂; *paratypes*, 7 ♂ ♀, with the allotype.

Prionocera primoveris is very different from the other regional species of the genus, differing especially in the short, triangular flagellar segments and in the structure of the male hypopygium, more especially of the tergite.

Nephrotoma lugens erythrophrys (Williston, 1893).—Yellowstone, July 14, 1930 (Amer. Mus. Nat. Hist., No. F. 300,714).

Tipula (*Schummelia*) *subtenuicornis* Doane, 1901.—Tower Falls, 6,500 ft., June 23 and 25, 1941; Obsidian Creek, 7,300 ft., June 27, 1941.

Tipula (*Yamatotipula*) *albocaudata* Doane, 1901.—Obsidian Creek, 7,300 ft., June 27, 1941.

Tipula (*Yamatotipula*) *continentalis* Alexander, 1941.—Tower Falls, 6,200 ft., abundant, June 26, 1941.

Tipula (Yamatotipula) colteri sp. nov.—Allied to *tephrocephala;* general coloration of mesonotum gray, the praescutum with three grayish brown stripes that are heavily bordered by blackish, the median stripe not or scarcely divided by a median vitta; antennae (male) relatively long, flagellum uniformly black; wings with a dusky tinge, stigma relatively small, brown; a brown seam in cell *M* adjoining vein *Cu*, continued over *m-cu;* male hypopygium with the paired tergal lobes entirely blackened, relatively short, the dorsal surface with conspicuous black setae throughout the length; inner dististyle complex, the beak subtriangular in outline, with almost the whole surface covered with microscopic setulae.

♂. Length, about 15-16 mm.; wing, 16-17.5 mm.; antenna, about 6.7-7 mm.

♀. Length, about 19-20 mm.; wing, 19-22 mm.; antenna, about 3.3 mm.

Frontal prolongation of head reddish brown, restrictedly variegated above and on sides by dark brown; nasus elongate; palpi black. Antennae of male elongate, of female much shorter; scape and pedicel reddish brown, flagellum black; flagellar segments (male) rather strongly incised; longest verticils shorter than the segments. Head brownish gray, clearer gray on front and orbits; vertex with a more or less distinct dark brown median vitta.

Pronotum dark reddish brown medially, brownish gray on sides; scutellum with a small yellow spot on either side; pretergites brownish gray. Mesonotal praescutum gray, with three more grayish brown stripes that are heavily bordered by blackish; median stripe relatively broad, not or only vaguely split by a dark median vitta; scutum gray, each lobe with two dark brown areas; scutellum and postnotum light gray, with vague indications of a capillary darker vitta; parascutella dark; lateral borders of mediotergite and much of katapleurotergite yellow. Pleura clear gray; dorsopleural membrane brownish yellow. Halteres with stem light brown, knob brownish black. Legs with coxae light gray; trochanters light brown; femora light brown, with rather narrowly blackened tips, the amount subequal on all legs; tibiae and basitarsi brown, their tips blackened; remainder of tarsi black. Wings with a dusky tinge, the prearcular and costal fields more brownish yellow; stigma relatively small, brown; a conspicuous brown seam along *m-cu* and vein *Cu* in cell *M;* a dark seam on anterior cord; other dusky clouds in cephalic portion of cell *R* and in outer radial field; obliterative areas before stigma and across base of cell *1st* M_2 restricted; base of cell R_2 slightly paler; veins brownish black, brighter in the paler costal and prearcular areas. Venation: *Rs* about twice *m-cu;* M_{3+4} subequal to or much shorter than the basal section of M_{1+2}.

Basal abdominal tergites yellow, the outer segments more obscure brownish yellow; a conspicuous black sublateral stripe on either side, widened on posterior segments; outer segments, including most of hypopygium, blackened, sparsely pruinose; outer dististyle pale; basal sternites more uniformly obscure yellow. Ovipositor with cerci long and slender, nearly straight. Male hypopygium (Fig. 3) with the tergal lobes, *9t,* entirely blackened, provided with abundant black spines at and near tip, together with conspicuous black setae on the entire remainder of dorsal surface. In *albocaudata,* the lobes are longer and more slender, blackened and provided with sparse black spines only at tips, the remainder of surface yellow and almost destitute of setae. Outer dististyle, *od,* relatively long and narrow, only a little widened at about midlength, the tip obtuse. Inner dististyle, *id,* complex, broad-based, the beak subtriangular in outline, provided with microscopic setulae over the entire surface excepting only the extreme margins; in addition to a flattened dorsal blade, there is a third flattened blade or flange on the face of the style. In *albocaudata,* the outer dististyle is strongly dilated at near midlength, the outer margin being strongly sinuate; beak of inner dististyle narrower and more elongate, the surface almost glabrous; dorsal blade of style very small, on its outer portion bearing a further flange or crest; the blade found on the face of the style in *colteri* is here not so clearly developed.

Holotype, ♂, Sylvan Lake, Yellowstone, 8,000 ft., June 21, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotype*, 1 ♂; *paratypes*, 15 ♂ ♀, Robson, British Columbia, 1,700 ft., May 9-23, 1937 (*H. Foxlee*). The series of paratypes agrees closely with the types and are considered to be conspecific.

Named for John Colter (1775-1813), the first white man to see either the Tetons or the Yellowstone. Colter was a member of the Lewis and Clark Expedition, 1803-1806. During the winter of 1807-1808, Colter, alone, with a thirty pound pack and rifle, travelled on snowshoes for more than 500 miles through the Absarokas, Jackson Hole, Tetons and the Yellowstone.

The nearest relative is *Tipula* (*Yamatotipula*) *albocaudata* Doane, 1901, which also occurred in Yellowstone as discussed elsewhere. The differences between the two flies include the structure of the antennae and male hypopygium, as well as the coloration of the praescutum and wings.

Tipula (*Yamatotipula*) *tephrocephala* Loew, 1864.—Emerald Pool, 7,275 ft., June 30, 1941. This is the first record of occurrence of this eastern species in the west.

Tipula (*Bellardina*) *subcinerea* Doane, 1901.—Gorge at base of Tower Falls, 6,200 ft., June 25 and 26, 1941 (*M. M. Alexander*); a few swept from dense coniferous growth.

Tipula (*Vestiplex*) *leucophaea* Doane, 1901.—Obsidian Creek, 7,300 ft., June 27, 1941 (*W. H. Harrison*); Tower Falls, 6,500 ft., June 23, 1941. This material agrees well with specimens from Colorado determined as being of this species except that the dark clouds on the wings are more extensive and slightly more intense, far exceeding in area the intervening whitish ground pattern. Antennae (male) much longer than in female; basal flagellar segments very weakly bicolored, the outer ones uniformly black; segments rather strongly incised.

Tipula (Oreomyza) absaroka sp. nov.—General coloration gray, the praescutum with four entire dark brown stripes; antennae (male) relatively short, scape obscure brownish yellow, remainder of organ black; anterior vertex broad, eyes relatively small; knobs of halteres dark brown; femora obscure brownish yellow, the tips narrowly blackened; claws (male) simple; wings with a strong brownish tinge, stigma darker brown; restricted obliterative areas before stigma and across cell *1st* M_2; abdominal tergites plumbeous gray, in male with a narrow obscure orange median stripe on segments two to four inclusive; in female, this stripe even longer and more conspicuous; ovipositor with long cerci; male hypopygium of unusually simple structure; ninth tergite nearly truncate across the caudal border, with a very small median notch; outer dististyle broadly flattened; inner dististyle simple; eighth sternite unarmed.

♂. Length, about 12-14 mm.; wing, 12-15 mm.; antenna, about 3-3.5 mm.

♀. Length, about 14-20 mm.; wing, 12-14 mm.

Frontal prolongation of head relatively short and stout, dark brown above, paler brown on sides; nasus conspicuous; palpi black. Antennae relatively short in both sexes, shorter in female; scape obscure brownish yellow, remainder of organ black; flagellar segments (male) short and crowded, moderately incised, the basal swelling shorter than the outer one; verticils shorter than the segments. Head gray, a little darker on the low vertical tubercle; eyes small, the anterior vertex correspondingly wide, approximately four times the diameter of scape.

Pronotum dark gray. Mesonotal praescutum light gray laterally, with four entire dark brown stripes, the intermediate pair separated by a capillary gray line; posterior interspaces more brownish yellow, with short yellow setae; posterior sclerites of notum light gray, each scutal lobe with two confluent dark brown areas; scutellum and mediotergite with indications of a capillary darker median vitta. Pleura light gray; dorso pleural membrane extensively buffy yellow. Halteres with stem obscure brownish yellow, knob dark brown. Legs with coxae light gray; trochanters obscure yellow; femora obscure brownish yellow, the tips narrowly blackened, more gradually and extensively so on the fore pair; tibiae black, obscure yellow basally; tarsi black; tibial spur formula 1-2-2; claws simple. Wings (Fig. 4) with a strong brownish tinge, the costal and prearcular fields more yellowish; stigma oval, darker brown; restricted whitish obliterative areas before stigma and again across the base of cell *1st* M_2, barely entering cell M_3; no post-stigmal brightening; in cases, certain of the cells, especially in outer medial field, with pale centers; veins brownish black, more yellowish brown in the brightened fields. Squama naked; veins R_{4+5} and outer branches of M with rather numerous macrotrichia. Venation: Rs relatively long, from one-third to one-half longer than *m-cu;* R_{1+2} entire; cell *1st* M_2 relatively small; *m-cu* at or close to fork of M_{3+4}.

Basal abdominal tergite plumbeous gray; on succeeding segments gray

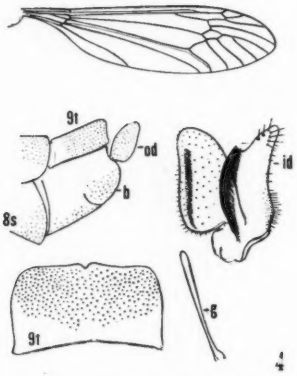


Fig. 4. *Tipula (Oreomyza) absaroka* sp.n.; male hypopygium. (Symbols: *g*, gonapophysis; *id*, inner dististyle; *od*, outer dististyle; *t*, 9th tergite.)

with an obscure orange median stripe that, in male, becomes obsolete about at the base of the fifth tergite; lateral tergal borders broadly obscure yellow, the extreme edges more whitened; outer segments more uniform brownish black, heavily pruinose; basal sternites suffused with reddish, the outer ones gray pruinose, with pale lateral borders; hypopygium brownish black. In female, the mid-dorsal yellow stripe is more conspicuous and continuous, extending from base of segment two to segment eight; genital shield brownish black. Ovipositor with cerci long, slender and nearly straight; hypovalvae shorter and more compressed. Male hypopygium (Fig. 4) of unusually simple organization, not enlarged. Ninth tergite separated from sternite by a complete suture; basistyle large, separated from ninth sternite by a ventral suture only. Ninth tergite, *9t*, large, transversely rectangular; caudal margin almost truncate, with a very small U-shaped median notch; caudal border of lobes blackened and microscopically corrugated. Outer dististyle, *od*, broadly flattened, provided with abundant short setae. Inner dististyle, *id*, unusually simple in structure, consisting of an elevated black dorsal crest and a simple beak that is provided with a few long setae. Gonapophyses, *g*, appearing as long and unusually slender spatulate rods. Eighth sternite, *8s*, unarmed.

Holotype, ♂, Twogwotee Pass, Grand Teton National Forest, 9,650 ft., July 9, 1942 (*C. P. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, numerous ♂♀; *paratypes*, ♂♀, Emerald Pool, Yellowstone, 7,275 ft., June 28-30, 1941, July 10 and 12, 1942; Grand Tetons, along Cascade Canyon trail, 8,500 ft., July 9, 1941 (*C. P. Alexander*), the latter in a small bog with much *Kalmia polifolia* Wang, *Menziesia ferruginea* Smith and *Phyllodoce empetriformis* (Smith) Don.

The nearest relative is *Tipula* (*Oreomyza*) *plutonis* Alexander, 1919, (Sequoia National Park, California, 9,000 ft.) which differs especially in the smaller size, distinct venational details, as the shorter *Rs* and petiole of cell M_1, and the apparent obliteration of the pale central praescutal vitta to leave only three clearly defined praescutal stripes, the great reduction in amount of reddish color on the abdominal tergites, and slight differences in the male hypopygium. I am not entirely satisfied with the subgeneric reference of these two flies. The structure of the dististyles and gonapophyses is somewhat as in *Yamatotipula* but I hesitate to refer these flies to this subgenus.

Tipula (*Oreomyza*) *neptun* Dietz, 1921.—Numerous specimens at Quad creek, Bear Tooth Mountains, 10,000-10,500 ft., August 15-19, 1942 (*J. L. & G. H. Sperry*); associated with *Tipula* (*Lunatipula*) *dens-ursi* sp. nov., *T.* (*L.*) *satyr* Alexander and *T.* (*L.*) *sperryana* Alexander.

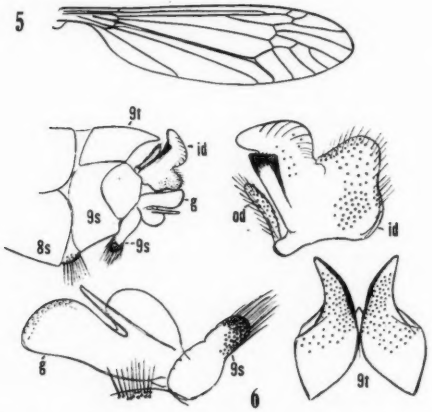
Tipula (Lunatipula) dens-ursi sp. nov.—General coloration of mesonotum gray, the praescutum with three brown stripes; antennae (male) of moderate length; flagellum black, pedicel obscure brownish yellow; femora obscure reddish yellow, the tips narrowly blackened; claws weakly toothed and conspicuously hairy; wings with a brownish gray tinge, the oval stigma dark brown; abdomen reddish yellow, the tergites with a conspicuous median black

stripe; outer abdominal segments more uniformly blackened; male hypopygium with the ninth tergite deeply notched, the lateral lobes long and conspicuous, divergent, with a tiny median denticle at base of notch; basistyle large, complete; inner dististyle with outer basal lobe very short and wide, broadly joined to the main body of style; gonapophyses projecting conspicuously from the genital chamber as compressed-flattened blades; eighth sternite unarmed but with a loose median tuft of more than a score of setae arising from the membrane between the eighth sternite and ninth sternite.

♂. Length, about 15 mm.; wing, 14 mm.; antenna, about 5-5.1 mm.

Frontal prolongation of head uniformly dark brownish gray, clearer gray on dorsal portion; nasus conspicuous, tufted with yellow setae; palpi dark brown, the extreme apices of segments pale. Antennae (male) relatively long, about one-third the length of body or wing; scape light brown; pedicel obscure brownish yellow, narrowly darkened on basal portion; flagellum uniformly black; flagellar segments only gently incised, subequal in length to their longest verticils. Head dark gray, more infuscated on central portion of vertex, narrowly clearer gray on front and orbits.

Pronotal scutum dark gray, the scutellum yellow. Mesonotal praescutum gray with three entire brown stripes that are relatively inconspicuous against the ground; setae of praescutal interspaces pale and rather short; scutum with lobes extensively infuscated, the central area broadly gray, with a narrow median dark brown line that further involves the scutellum; posterior sclerites of notum light gray, the parascutelia darker; pleurotergite with the katapleurotergite abruptly differentiated in color from the anapleurotergite, the cephalic



Figs. 5, 6. *Tipula (Lunatipula) dens-ursi* sp.n.; venation and male hypopygium. (Symbols: *g*, gonapophysis; *id*, inner dististyle; *od*, outer dististyle; *s*, sternite; *t*, 9th tergite.)

half whitish silvery, the posterior portion more bicolored, its dorsal section light brownish yellow, the ventral portion dark brown, sparsely pruinose. Pleura clear light gray, the ventral portion of dorsopleural membrane narrowly buffy, the dorsal portion gray pruinose. Halteres with stem obscure brownish yellow, knob darkened. Legs with coxae and trochanters brown, light gray pruinose; femora obscure reddish yellow, the tips narrowly blackened, the amount subequal on all legs; tibiae obscure yellowish brown, passing into black at tips; tarsi black; claws conspicuously hairy, with a low basal tooth; empodia long, conspicuously hairy. Wings (Fig. 5) with a strong brownish gray tinge; stigma oval, dark brown; veins brownish black. Squamal setae at least six in number; veins beyond cord with normally developed series of trichia; vein R_{1+2} with trichia on proximal half; no stigmal trichia. Venation: R_{1+2} deflected strongly cephalad on distal half, widening the cell; basal section of M_{1+2} longer than M_{3+4}; petiole of cell M_1 about one-third to one-half longer than *m*.

Abdominal tergites reddish yellow, with a conspicuous median black stripe that is narrowly interrupted on the posterior borders of the segments; sublateral stripes not or but vaguely indicated; basal sternites more uniform reddish yellow, on the sixth and succeeding segments more uniformly darkened, the outer three segments black, segments six and seven with very narrow yellow posterior borders. Male hypopygium (Fig. 6) with the tergite entirely separate from the sternite. Basistyle, *b*, complete, unusually large, not produced at apex. Ninth sternite, *9s*, with no accessory sclerites cut off cephalad of basistyle. Ninth tergite, *9t*, with caudal border produced into two elongate, weakly divergent lobes or blades, separated by a very narrow V-shaped notch, at base of which is a very small, paler, chitinized denticle; lateral tergal lobes with their mesal edges more or less flattened and produced into a flange; dorsal surface of tergite with a deep and narrow furrow; cephalic border of sclerite deeply emarginate or notched, with pale membrane. Outer dististyle, *od*, small, weakly flattened and compressed, provided with relatively few setae. Inner dististyle, *id*, with apex of main body heavily blackened, the tip and dorsal border evenly rounded, without points or angles; outer basal lobe, *obl*, large and very broadly joined to the main body of style. Lobes of ninth sternite, *9s*, conspicuous, hanging pendant in the notch of sternite, the distal portion more blackened and bearing a dense brush of long yellow setae. Gonapophyses, *g*, appearing as unusually conspicuous flattened yellow blades that jut caudad from the genital chamber. Eighth sternite, *8s*, unarmed, not sheathing; in membrane between the eighth and ninth sternites a median area or loose tuft of more than thirty setae, directed chiefly ventrad, disposed in two more or less distinct subgroups.

Holotype, ♂, Bear Tooth Mountains, Montana; Quad Creek, 10,000 ft., August 13, 1942 (*J. L. & G. H. Sperry*); swept from among dwarf willows.

This very distinct species appears to be closest to *Tipula* (*Lunatipula*) *sperryana* Alexander, from exactly the same geographical and ecological situation. It differs from the latter in every regard of coloration, venation and structure of the male hypopygium. The four Arctic-Alpine species of *Tipula*

taken by Mr. and Mrs. Sperry at high altitudes in the Bear Tooth Mountains on the border of Wyoming and Montana present the best idea we have yet had of such a fauna. All four of the species of *Tipula* so taken are evidently adapted to an existence under high alpine conditions, occurring among the scrub willows and 'Krummholz' at these high altitudes.

Tipula (*Lunatipula*) *sperryana Alexander,* 1942.—The types were from Frozen Lake, 10,000 ft., in the Bear Tooth Mountains. Further material was taken in 1942 from this general vicinity, Quad Creek, 10,000-10,200 ft., August 13-19, 1942 (*J. L. & G. H. Sperry*). Further notes on the male hypopygium, and a description of the hitherto unknown female are given.

Male hypopygium (Fig. 7) with the ninth tergite, *9t,* entirely separated from the sternite. Basistyle, *b,* large, more or less distinctly separated from the sternite by a suture. Ninth tergite, *9t,* large and conspicuous, yellow, patterned with dark brown; broadest at base, narrowed outwardly, the caudal margin deeply emarginate, the lateral lobes produced into long, relatively narrow, pale blades, their tips narrowly obtuse to subacute, without conspicuous setae; at base of notch with a smaller slender median lobe that is densely covered with short erect setulae. Basistyle, *b,* at apex produced into a broad flattened blade, its tip obtuse. Outer dististyle, *od,* a conspicuous flattened spatula. Inner dististyle, *id,* with the main body large, compressed-flattened, the apex and dorsal crest evenly rounded; outer basal lobe, *obl,* very large and conspicuous, pale, of irregular conformation, provided with numerous strong setae from elevated basal tubercles. A close group of sensory pits near base of the outer lobe, immediately caudad of which is a conspicuous longitudinal row or group of more elongate setae. Ninth sternite, *9s,* with conspicuous oval lobes that are densely provided with long yellow setae. Gonapophyses, *g,* appearing as unusually large, flattened-compressed yellow blades that jut conspicuously beyond the genital chamber. Eighth sternite, *8s,* unarmed.

Allotype, ♀, Quad Creek, 10,000 ft., August 15, 1942.

♀. Length, about 20 mm.; wing, 13.5 mm.; antenna, about 3 mm.

Characters as in male, differing chiefly in the sexual characters. Antennae much shorter; flagellar segments cylindrical or nearly so, the basal enlargements scarcely evident; longest verticils subequal in length to the segments; terminal segment without verticils, abruptly narrowed at tip. Legs much shorter and stouter than in male; femora somewhat more extensively blackened. Wings proportionately a little shorter but with no distortion of the venation. Abdomen slightly elongated. Ovipositor with genital shield blackened; cerci brownish yellow, elongate, relatively broad, compressed-flattened, their tips acute, margins smooth; hypovalvae shorter than the cerci, extending about to three-fourths the length of the latter, their tips rounded.

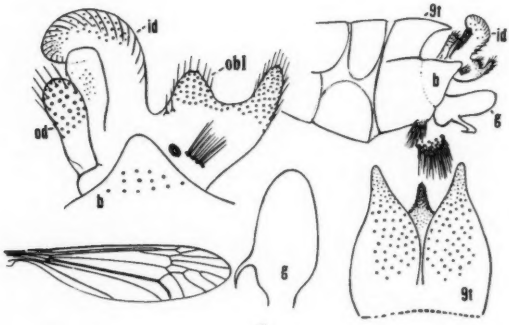
Tipula (*Lunatipula*) *pleuracicula* Alexander, 1915 (*monochroma* Dietz, 1919).—Tower Falls, 6,500 ft., along creek, June 25, 1941; Northeast Entrance, 7,200 ft., June 24 and 26, 1941.

Tipula (*Lunatipula*) *satyr* Alexander, 1915, ♂; (*claasseni* Alexander, 1920, ♀).—The holotype of *satyr* was from an unknown locality in Colorado,

contained in the C. V. Riley Collection in the United States National Museum, and was presumed to have been taken by Henry K. Morrison. The type of *claasseni* was from Lawn Lake in the Mummy Range, Rocky Mountain National Park, Colorado, 11,000 ft., collected August 27, 1919, by the late Dr. P. W. Claassen. The two sexes are so different from one another in their general appearance that it was necessary to take both at the same time and place, or in copula, in order to settle their identity. Several specimens of both sexes were taken by Mr. and Mrs. Sperry at Quad Creek, Bear Tooth Mountains, Montana, 10,200 ft., August 19, 1942, and the synonymy is certain.

The species belongs to the *bicornis* (*fascipennis*) group but is entirely distinct from the five species of the group hitherto described from the Nearctic region. All such occur in northern and eastern North America. Among such species, the present fly is most similar to *Tipula* (*Lunatipula*) *parshleyi* Alexander, 1915, yet entirely distinct. The present species is now known from Colorado, the high mountains of the Montana-Wyoming border and recurs in the highest mountains of central Gaspé in eastern Quebec.

Male hypopygium (Fig. 8) with the ninth tergite, *9t*, separated from the sternite by a suture that is lost only at the extreme cephalic portion of the sclerite. Basistyle, *b*, incompletely separated from the sternite, the suture indicated on the dorsal and ventral portions. Total area of basistyle and ninth sternite much restricted by the large eighth sternite. Ninth tergite, *9t*, subquadrate, the caudal border gently and sinuously emarginate, with a further very deep, parallel-sided median notch, the lateral lobes produced into strong horn-like points; on dorsal surface of tergite, on outer half and closer to the lateral border than to the midline, an even longer reddish horn that is directed chiefly caudad; dorsal surface of tergite behind the median split with an impressed furrow, the adjoining surfaces with a concentration of strong setae, lacking on



7

Fig. 7. *Tipula (Lunatipula) sperryana* Alexander; venation and male hypopygium. (Symbols: *b*, basistyle; *g*, gonapophysis; *id*, inner dististyle; *obl*, outer basal lobe of inner style; *od*, outer dististyle; *s*, sternite; *t*, 9th tergite).

Fig. 8. *Tipula (Lunatipula) satyr* Alexander; male hypopygium and ovipositor. (Symbols: *b*, basistyle; *cer*, cercus; *d*, dististyle; *g*, gonapophysis; *h*, hypovalvae; *s*, sternite; *t*, 9th tergite.)

cephalic portion of sclerite, reduced to small scattered setulae on the broad outer tergal plates. Dististyle, *d*, of irregular conformation; outer basal lobe, *obl*, subequal in size to the main body of style and not differing greatly therefrom in shape; surface of this lobe provided with abundant, very long and delicate setae that are directed outward and backward. From the dorso-mesal angle of the ninth sternite, *9s*, juts caudad a long, gently sinuous, cylindrical rod that is provided with numerous long setae that are directed chiefly ventrad. Gonapophyses, *g*, blackened, projecting conspicuously from the genital chamber, their basal portions straight, directed caudad, the long acute tips directed strongly ventrad. Eighth sternite, *8s*, large and conspicuously sheathing; outer lateral angles cut off by sutures into small oval lobes, each terminating either in two or in three very powerful blackened spines but without surface setae; median area of border with additional smaller setae, including a central group that are directed mesad, placed on either side of a small conical median lobule.

Ovipositor (Fig. 8) with both cerci, *cer*, and hypovalvae, *h*, very short, the former appearing as blunt fleshy lobes, their caudal margin oblique, provided with an abundant short setae and scattered longer ones. Hypovalvae appearing as pale, compressed-flattened blades, the apex of each irregularly toothed, the most dorsal point or denticle largest. The abdomen of the female studied was filled with unusually large black eggs having very heavy chorion.

CYLINDROTOMINAE

Cylindrotoma pallescens Alexander, 1930.—Northeast Entrance, 7,200 ft., June 24 and 26, 1941; Obsidian Creek, 7,300 ft., June 27, 1941.

LIMONIINAE

LIMONIINI

Limonia (*Limonia*) *indigena jacksoni* (Alexander, 1917).—Tower Falls, 6,500 ft., June 25, 1941.

Limonia (*Limonia*) *sciophila* (Osten Sacken, 1877).—Tower Falls, 6,500 ft., June 25, 1941; Northeast Entrance, 7,200 ft., June 24, 1941.

Limonia (*Metalimnobia*) *solitaria* (Osten Sacken, 1859).—Tower Falls, 6,500 ft., June 26, 1941; Northeast Entrance, 7,200 ft., June 24, 1941.

Limonia (*Dicranomyia*) *brevivena* (Osten Sacken, 1869).—Emerald Pool, 7,275 ft., June 29, 1941.

Limonia (*Dicranomyia*) *morioides* (Osten Sacken, 1860).—Northeast Entrance, 7,200 ft., June 24, 1941.

Limonia (*Dicranomyia*) *nycteris* (Alexander, 1927).—Northeast Entrance, 7,200 ft., June 24, 1941.

Limonia (*Dicranomyia*) *penicillata* (Alexander, 1927).—Obsidian Creek, 7,300 ft., June 27, 1941; Upper Geyser Basin, near the Giant Geyser, 7,300 ft., June 29, 1941.

Limonia (Dicranomyia) geyserensis sp. nov.—Allied to *haeretica;* general coloration of male gray, of the female more ocherous; rostrum dark brown; antennae black throughout; mesonotal praescutum with a conspicuous brownish black median stripe; knobs of halteres dark brown; legs chiefly dark brown; wings of male fully developed, of female reduced to microscopic scales; in male, vein Sc_1 relatively long; male hypopygium with the rostral prolongation moderately deep, the two spines placed less than their own length apart.

♂. Length, about 6-6.5 mm.; wing, 6-7 mm.

♀. Length, about 6 mm.; wing, 1.5 x 0.3 mm.

Rostrum and palpi dark brown. Antennae black throughout; flagellar segments subglobular to short-oval, the outer segments passing through oval to elongate-oval. Head dark gray, the anterior vertex weakly infuscated; anterior vertex (male) a little less than three times the diameter of scape.

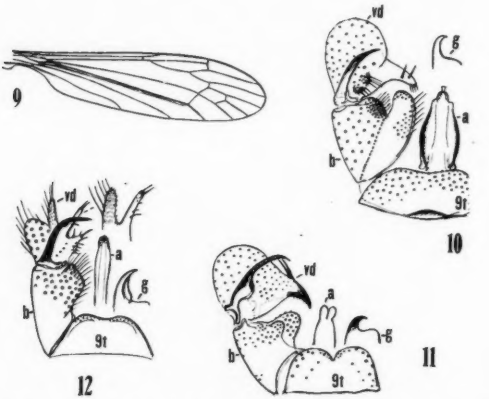
Pronotum broadly blackened medially, narrowly ocherous on sides, the scutellum more broadly so. Mesonotum light gray, the praescutum with a broad brownish black median stripe that becomes obsolete at near two thirds the length of the sclerite; lateral stripes obsolete; in female, the ground color of notum more ocherous but the pattern of praescutum identical; posterior sclerites of notum heavily pruinose in male, the posterior border of scutellum more ocherous; in female, the posterior notum more ocherous. Pleura gray pruinose in male, more ocherous in female. Halteres short, stem yellow, knob dark brown. Legs with the coxae obscure yellow, the fore and middle pairs slightly more darkened; femora, tibiae and basitarsi dark brown, restrictedly brightened at their bases, the tips conspicuously blackened; remainder of legs black. Wings of male (Fig. 9) fully developed, with a weak brown tinge, the

prearcular field more whitened; stigma not or scarcely darkened; veins brown. Venation: Sc_1 ending a short distance beyond origin of Rs, Sc_2 some distance from the tip of Sc_1 so the latter vein is unusually long for a member of this group, approximately equal in length to vein R_{2+3}; *m-cu* close to the fork of *M*. In female, the wings are reduced to microscopic scales, as shown by the measurements; main stem of *R* preserved and with a series of macrotrichia extending back to arculus; a linear row of setae in the membrane about where vein R_{2+3} is normally present but with no indication of the vein itself; cubital vein preserved as a more or less distinct thickening but without macrotrichia. Wings about two and one-half times as long as the halteres. Venation: Prearcular field unusually long, occupying more than the basal fourth of the entire wing.

Abdominal tergites brown medially, paling to brownish yellow on sides; subterminal segments more uniformly and extensively darkened; sternites obscure yellow, with a narrow subterminal brown ring; hypopygium chiefly yellow. Male hypopygium (Fig. 10) of the general type of *haeretica* and *penicillata*. Dorsal dististyle relatively narrow, its distal fourth narrowed into a slender apical spine. Ventral dististyle, *vd*, with the setae on mesal face at base arranged in two distinct groups but not forming pencils; rostral prolongation moderately deep, the two spines placed less than their own length apart.

Holotype, ♂, Yellowstone, near the Giant Geyser, 7,300 ft., June 29, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, 6 ♂♂, with the type; *paratype*, 1 ♂, Emerald Pool, 7,275 ft., July 10, 1942.

The types were swept from low rushes near the geyser. Here they were



Figs. 9, 10. *Limonia (Dicranomyia) geyserensis* sp. n.; venation and male hypopygium. Fig. 11. *Limonia (Dicranomyia) fulva fulvoides* subsp.n., male hypopygium. Fig. 12. *Limonia (Alexandriaria) phalangioides* sp.n.; male hypopygium. (Symbols: *a*, aedeagus; *b*, basistyle; *g*, gonapophysis; *t*, 9th tergite; *vd*, ventral dististyle.)

found crawling about near the ground, associated with several species of Saldid bugs and with Carabid beetles of the genus *Elaphrus*.

The present insect is of unusual interest in that it is one of two species of the vast genus *Limonia* Meigen found in the Yellowstone (compare also *Limonia phalangioides* sp. nov.) in which the wings of one or both sexes are greatly reduced, a condition not before known in any Nearctic member of the genus. In the present species it is only the female that has the wings so reduced but here the degeneration is profound and by the scale of classification proposed by Bezzi (Riduzione e scomparsa delle ali negli insetti ditteri. Rivista di scienze naturali, "Natura," 7: 85-182, 11 figs.; 1916) would fall in his group 5, including species having squamiform wings with indistinct venation and distinctly longer than the halteres, giving the insect somewhat of a nymphal aspect. It should be noted that in both of these subapterous *Limonia* species the wings, in addition to being much reduced in size are of the stenopterous type, long and narrow, and that consequently the reduction of area is considerably greater than in the case of a brachypterous wing of the same length.

Despite the uniqueness of the character of wing reduction in the female, the fly is closely related to *Limonia* (*Dicranomyia*) *haeretica* (Osten Sacken, 1869) and *L.* (*D.*) *penicillata* (Alexander, 1927), both of which are fully-winged in both sexes. The structure of the male hypopygium in all three of these species is generally alike though differing in minor details. The males of the present fly are most readily told from such allies by the conspicuous gray body coloration, the dark brown rostrum, conspicuously darkened legs, and by the unusually long vein Sc_1. In *penicillata*, the rostral prolongation of the ventral dististyle is long and relatively narrow, with the outer spine placed more than its own length from the tip; setae at base of mesal face of ventral dististyle forming two conspicuous brushes or pencils.

Limonia (*Dicranomyia*) *athabascae* (Alexander, 1927).—Obsidian Creek, 7,300 ft., June 27, 1941; Elk Park, 7,000 ft., June 28, 1941; Emerald Pool, 7,275 ft., June 29 and 30, 1941; one of the most abundant and characteristic crane-flies in all three stations. Not before recorded from the United States.

Limonia (Dicranomyia) fulva fulvoides subsp. nov.—Mesonotum almost uniformly dark brownish gray, without clearly defined stripes; antennae black throughout; halteres pale, the knobs weakly darkened; male hypopygium with the ninth tergite deeply notched medially; gonapophyses with mesal-apical lobe strongly curved, its blackened tip acute.

♂. Length, about 6.5-7 mm.; wing 7.6-8.5 mm.

♀. Length, about 7-7.5 mm.; wing, 7.5-8 mm.

Rostrum light brown; palpi brownish black. Antennae black throughout; basal flagellar segments short-oval, the outer ones longer; verticils a little shorter than the segments. Head gray; anterior vertex of moderate width, a little more than twice the diameter of scape.

Pronotum dark brownish gray. Mesonotum almost uniform dark brownish gray, the praescutum without clearly defined stripes; scutellum and median region of scutum a little paler. Pleura slightly more testaceous, sparsely pruinose. Halteres short, stem pale, knob weakly darkened. Legs with the coxae and trochanters yellow; femora obscure yellow, their tips scarcely darker; tibiae and proximal segments of tarsi brownish yellow, the outer tarsal segments black. Wings with a very faint grayish tinge, the prearcular field more whitened; stigma oval, pale brown, inconspicuous; veins brown, those in the prearcular field more whitened. Venation: Sc_1 ending a short distance beyond origin of *Rs*, Sc_2 a short distance from its tip; *Rs* weakly angulated to short-spurred at origin; *m-cu* at or close to fork of *M*.

Abdominal tergites and outer sternites dark brown, the basal sternites and hypopygium more yellowish. Male hypopygium (Fig. 11) with the ninth tergite, *9t*, extensive, deeply notched medially, the lobes broadly rounded; outer margin of lobes thickened; setae chiefly marginal, those toward the median notch smaller but abundant. Basistyle, *b*, with the ventromesal lobe simple, at its base with a smaller accessory lobule. Dorsal dististyle widely dilated near base, suddenly narrowed into a slender blackened rod, the acute tip decurved. Ventral dististyle, *vd*, of moderate size, its total area about equal to that of the basistyle; rostral prolongation blackened and acute at apex; rostral spines two, placed close together near base of rostrum, a little shorter than the remainder of style beyond the point of their insertion. Gonapophyses with mesal-apical lobe strongly curved, the blackened tip acute.

Holotype, ♂, Lewis Lake, Yellowstone, July 1, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, 3♀♀, with the types (*W. H. Harrison*); *paratypes*, ♂♀, Canyon Camp, 7,800 ft., June 21, 1941; Emerald Pool, 7,275 ft., July 12, 1942 (*C. P. Alexander*).

Typical *fulva* (Doane, 1900) is known to me only from the original description and from a carefully drawn figure of the hypopygium of the unique male of the type series (Pullman, Washington). I am greatly indebted to Dr. Henry Townes for making this drawing and certain others. The Yellowstone material differs from the description and figure in certain details that seem to make it inadvisable to determine the material as being typical *fulva*. Doane describes his species as being yellowish, but in the present fly there is little or no yellow coloration; antennae black throughout; halteres with darkened knobs; male hypopygium with the ninth tergite more deeply notched; mesal-apical lobe of gonapophysis acutely pointed and blackened at tip.

Limonia (*Dicranomyia*) *halterata* (Osten Sacken, 1869).—Northeast Entrance, 7,200 ft., June 24 and 26, 1941; numerous.

Limonia (*Dicranomyia*) *humidicola* (Osten Sacken, 1859) (*badia* of authors, nec Walker, 1848).—Northeast Entrance, 7,200-7,300 ft., along small mountain stream, abundant, June 26, 1941; Emerald Pool, 7,275 ft., June 29, 1941.

Limonia (Alexandriaria) phalangioides sp. nov.—Allied to *whartoni;*

wings reduced to mere pads that are only about one-half longer than the halteres, their shape and venation greatly distorted; legs long and slender; male hypopygium with the lateral lobe of ventral dististyle provided with abundant delicate setulae, in addition to a few long conspicuous setae.

♂. Length, about 5 mm.; wing, about 1 mm. Fore leg; femur, 5 mm.; tibia, 5.3 mm.; tarsus about 4.8 mm; leg total, 15.1 mm.

Mouth parts, including palpi, brown; maxillary palpi with the three outer segments subequal in length, elongate-oval. Antennae with the scape brown, the pedicel and flagellum still darker brown; flagellar segments oval, the outer ones becoming more elongate and with progressively narrower points of connection between the segments. Head brown, extensive; anterior vertex about twice the diameter of the scape.

Pronotum dark brown medially, obscure yellow on sides. Mesonotum strongly gibbous, obscure yellow laterally, the praescutum with a conspicuous, dark brown, median stripe on cephalic portion, this becoming obsolete some distance before the suture; lateral praescutal stripes not indicated; posterior sclerites of notum obscure buffy yellow, the posterior portion of mediotergite restrictedly darkened. Pleura uniform buffy yellow. Legs unusually long and slender when compared to the length of body; coxae and trochanters yellow; remainder of legs brownish black to black, the femoral bases restrictedly obscure yellow; claws very long and slender, only gently curved, provided with a single long spine at about one-fourth the length. Wing of male greatly reduced in size, about one-half longer than the halteres, pale basally, the outer portion more suffused with dusky; wings strongly bent or angulated at about one-third the length; only two longitudinal veins persist, which from their positions apparently represent *R* and *Cu*, the former with a complete series of strong macrotrichia, these totalling about 35 in number; the supposed vein *Cu* glabrous; in the field between these two veins a few isolated trichia in longitudinal rows, evidently pertaining to the outer radial and medial veins.

Abdominal tergites reddish brown, with indications of a median brown stripe, deepest in color on the basal segment; sternites a trifle paler; hypopygium yellow. Male hypopygium (Fig. 12) of the general type of *whartoni*. Ninth tergite, *9t*, with the caudal margin very gently emarginate, the lobes very low, each with about a score of long setae. Basistyle, *b*, with the ventromesal lobe lying far distad, subrectangular in outline, covered with abundant coarse setae. Dorsal dististyle a long curved rod, gradually narrowed to the acute tip. Ventral dististyle, *vd*, of irregular conformation, as in *whartoni;* body of style small; outer paired lobes elongate, the lateral one with about seven or eight long setae and abundant, more delicate setulae, these latter lacking in *whartoni;* inner lobe subequal in length but more slender, terminating in two strong setae and with fewer ordinary setae throughout the length, some of the latter very small. Gonapophyses, *g*, with a conspicuous flange in the curve of the mesal-apical lobe.

Holotype, ♂, Emerald Pool, 7,275 ft., July 10, 1942 (*C. P. Alexander*).

The unusual insect described above is of exceptional interest. It is the first member of the genus *Limonia* in the Nearctic fauna in which the male sex is nearly apterous (compare *Limonia geyserensis* sp. nov., in which the wings of the female only are somewhat similarly reduced). The general appearance of the present fly is much like a small harvestman or Phalangid, whence the specific name. Superficially the fly suggests one of the subapterous species of the Pediciine genera *Dicranota* Zetterstedt and *Polyangaeus* Doane, and when I first captured the unique type specimen, I believed it represented still another member of this tribe. The structure of the male hypopygium proves conclusively that it belongs to the subgenus *Alexandriaria* Garrett, 1922, and is closest to the only species that has been found in northeastern North America, *whartoni* (Needham, 1908). The nearly apterous condition will readily separate the fly from the various related species or forms, all of which are fully winged in both sexes. Although only a single male is known, it is virtually certain that the female has the wings reduced in similar manner. No Tipulid fly has ever been discovered having subapterous males and fully winged females. By Bezzi's scale of wing-reduction in the Diptera (reference cited under *Limonia geyserensis*), this fly likewise falls in his group 5, as defined earlier.

I captured the fly by sweeping rank herbage along the small stream in Study Area 7, defined earlier. The specimen had crawled up a plant to a height of more than a foot and was not observed until found in the net. The chances of finding specimens of such a flightless insect seem very slight.

Limonia (*Geranomyia*) *diversa* (Osten Sacken, 1859).—Emerald Pool, 7,275 ft., abundant, June 29 and 30, 1941; July 10 and 12, 1942.

Limonia (*Geranomyia*) *canadensis* (Westwood, 1835).—Emerald Pool, 7,275 ft., June 29 and 30, 1941.

Antocha (*Antocha*) *monticola* Alexander, 1917.—Along the Gibbon River, near Elk Park, 7,000 ft., June 28, 1941 (*W. H. Harrison*).

PEDICIINI

Ula paupera Osten Sacken, 1869.—Emerald Pool, 7,400 ft., July 12, 1942; swept from small alpine firs.

Ornithodes harrimani Coquillett, 1900.—Sylvan Lake, 8,000 ft., June 21, 1941; a single male specimen flying along a small mountain stream in lodgepole pine forest. The first record of the genus or species from the United States. Described from a unique male taken at Prince William Sound, Alaska, June 22, 1899, by Kincaid; later taken at Juneau, Alaska (1901, *de Joannis*, in Paris Museum) and at Laggan, Alberta (July 16, 1928, *Owen Bryant*).

Pedicia (*Tricyphona*) *sparsipuncta* (Alexander, 1920). — Northeast Entrance, 7,200 ft., June 24, 1941. There appears to be a considerable range in the relative diameter of the lateral arms of the ninth tergite of the hypopygium in various specimens that have been referred to this species.

Pedicia (*Tricyphona*) *aperta* (Coquillett, 1905).—Emerald Pool, 7,275 ft., July 12, 1942.

Dicranota (*Dicranota*) *montana* Alexander, 1920.—Northeast Entrance, 7,200 ft., June 24, 1941.

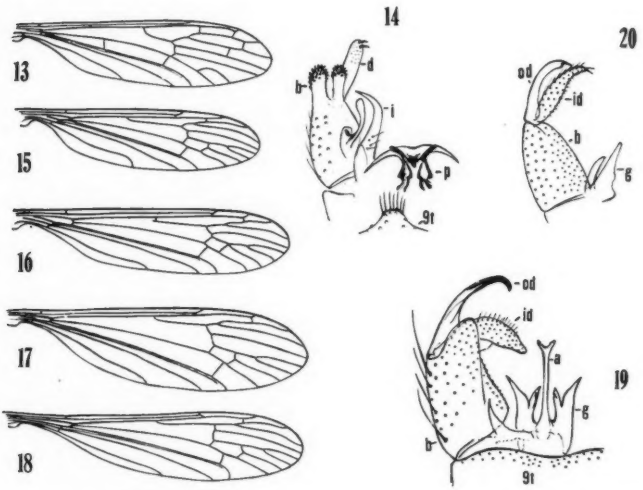
Dicranota (*Rhaphidolabis*) *cayuga* (Alexander, 1916). — Northeast Entrance, 7,200 ft., June 26, 1941. One male is of unusual size (Length about 6 mm.; wing, 8 mm.).

Polyangaeus subapterogyne sp. nov.—Sexes dimorphic; males fully winged, females subapterous; mesonotal praescutum brownish yellow laterally, the central portion deepening to a more or less distinct brown stripe; antennae (male) short, 12-segmented.

♂. Length, about 3-3.5 mm.; wing, 4-5 mm.

♀. Length, about 3-3.5 mm.; wing, about 0.8-1.1 mm.

Male. Rostrum and palpi dark brown. Antennae unusually short, 12-segmented; basal flagellar segments very short and crowded, with short verticils. Head dark grayish brown; eyes relatively small; anterior vertex broad, exceeding in width the visible diameter of a single eye.



Figs. 13, 14. *Polyangaeus subapterogyne* sp.n.; venation and male hypopygium. Fig. 15. *Pseudolimnophila vidua* sp.n.; venation. Fig. 16. *Limnophila* (*Phylidorea*) *nycteris* sp.n.; venation. Fig. 17. *Limnophila galactopoda* sp.n.; venation. Fig. 18. *Pilaria phaeonota* sp.n.; venation. Fig. 19. *Limnophila (Phylidorea) nycteris* sp.n.; male hypopygium. Fig. 20. *Pilaria phaeonota* sp.n.; male hypopygium. (Symbols: *a*, aedeagus; *b*, basistyle; *g*, gonapophysis; *i*, interbase; *id*, inner dististyle; *t*, 9th tergite.)

Pronotum yellow, weakly patterned with brown. Mesonotal praescutum brownish yellow, darkening to produce a brown median stripe, most distinct on cephalic half of sclerite, the lateral portions much paler; posterior sclerites of notum obscure yellow, without markings. Pleura obscure yellow, weakly darkened on ventral sternopleurite and meron; dorsopleural region even clearer yellow. Halteres dark brown, the basal fourth of stem yellow. Legs with the coxae and trochanters pale yellow; femora pale yellow, the tips conspicuously blackened; tibiae white, the extreme base and slightly wider tip blackened; tarsi brownish black, the proximal portion of basitarsi slightly paler. Wings (Fig. 13) relatively narrow, grayish subhyaline, weakly patterned with light brown, distributed as follows: Sc_2, tip of Sc_1; R_2 and the supernumerary crossvein in cell R_1; cord and fork of M_{3+4}; over the supernumeraries in the various cells; veins pale brown, a trifle darker in the clouded areas. Venation: Supernumerary crossveins in cells R_1, R_3, R_4 and M; considerable variation and abnormalities of venation occur in the type series, the chief of which are as follows.—Cell M_1 present or lacking, as shown in figure; in cases with only the base of vein M_2 atrophied, the tip lying free in membrane; in cases, the supernumerary crossvein in cell R_4 lacking; in even rarer instances the base of vein M_3 is atrophied and the supernumerary crossvein in cell R_1 may lie before the fork of R_{2+3+4}.

Basal abdominal tergites bicolored, obscure brownish yellow, the posterior borders darker brown; outer segments, including hypopygium, more uniform dark brown to brownish black. Male hypopygium (Fig. 14) with the median region of tergite, *9t*, produced into a conspicuous entire lobe that is provided with about ten long setae, grouped chiefly on extreme apical portion; lateral tergal arms produced into a flattened blade that is further narrowed into a glabrous cultrate to obtuse rod. Basistyle, *b*, at apex produced into two subequal lobes that are set apically with abundant blackened spines; interbase, *i*, a flattened yellow blade that narrows to a powerful curved spine, the surface with abundant microscopic setulae; near proximal portion of interbase with about four conspicuous setigerous punctures arranged in a more or less straight row. Dististyle, *d*, a flattened pale blade, the apex obtuse, provided with two strong spinous setae; other smaller setae over the surface, chiefly near apex; at base of style with a small appressed lobe or tubercle that terminates in a single powerful seta. Phallosome, *p*, appearing as a conspicuous blackened structure that terminates in two strongly divergent blackened rods; what appears to represent a part of the phallosome consists of two very strongly divergent horns that are straight or slightly decurved.

Female. Differs from male in sexual characters. Wings reduced to narrow pads, the venation chiefly atrophied; marginal setae of costal and anal regions conspicuous. Ovipositor with the valves, especially the cerci, of unusual size and development.

Holotype, ♂, Hidden Falls, Grand Teton National Park, 7,000 ft., July 4, 1941 (*M. M. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, several of both sexes with the types; *paratypes*, 1 ♂, Leigh Lake, Grand

Tetons, 6,875 ft., July 10, 1941; Moran, bog, near Grand Tetons, 6,800 ft., July 2, 1941; Yellowstone, Obsidian Creek, 7,300 ft., June 27, 1941; Emerald Pool, 7,275 ft., June 29 and 30, 1941.

Polyangaeus subapterogyne differs from the only other species so far described, the genotype, *maculatus* Doane, 1900, in the very short 12-segmented antennae, the narrower wings of the male, and in the details of coloration and the structure of the male hypopygium. I have no data to indicate whether or not the female of *maculatus* is subapterous or fully winged. I possess a third, still undescribed species of *Polyangaeus* from the Grand Teton National Forest that is fully winged in both sexes.

This is the third undescribed species discovered in the Yellowstone survey that was subapterous in either the female or in both sexes. By Bezzi's scale of classification of wing reduction and apterism in the Diptera (cited under account of *Limonia geyserensis* sp. nov.), the present fly falls in group 5, as was the case with the two species previously considered.

In the Yellowstone, only males were taken at Obsidian Creek; the first discovered female was swept from rank herbage along the stream at Emerald Pool. In the Grand Tetons, near Hidden Falls, a large series of both sexes was found on shaded earthen banks along the trail where there was a dense growth of mosses and foliaceous liverworts, the bank being shaded by alpine fir; *Ribes*, especially *parvulum* (Gray) Rydb.; *Bossekia parviflorus* (Nuttall); *Sorbus scopulina* Greene; *Acer glabrum* Torrey, and other characteristic plants. The females were found by us only when we lay prostrate on the ground and detected them crawling about over the beds of mosses and liverworts in very moist situations.

HEXATOMINI

Archilimnophila subunica (Alexander, 1920). — Yellowstone, Canyon Station, 8,000 ft., July 4, 1924 (*J. S. Alexander*); Northeast Entrance, 7,200 ft., June 26, 1941; near Sylvan Lake, 8,000 ft., July 13, 1942.

Pseudolimnophila vidua sp. nov.—General coloration, the praescutum dark gray with a single broad median brown stripe; pleura clear light gray; femora with tips broadly black, widest on fore legs, narrower on posterior pair where about the distal half is included; wings with a strong brown tinge, unpatterned; *Rs* long; abdomen black, the sternites more pruinose.

♀. Length, about 8-8.5 mm.; wing, 8-9 mm.

Rostrum gray; palpi black. Antennae black throughout, the scape sparsely pruinose; flagellar segments passing through oval to elongate; verticils of outer segments conspicuous. Head light gray.

Thoracic dorsum black, gray pruinose, the praescutum with a single broad median brown stripe, the lateral stripes not or scarcely defined. Pleura light gray pruinose. Halteres obscure yellow to weakly dusky, the knobs darker. Legs

with the coxae gray; trochanters brownish yellow; femora obscure yellow basally, the tips very extensively black, on the fore pair including the distal three-fourths or more, on the posterior legs involving the outer half; tibiae dark brown, the posterior pair more yellowish brown, their tips narrowly blackened; tarsi black. Wings (Fig. 15) with a strong brownish tinge, virtually unpatterned, the oval stigma only a trifle darkened; centers of cells *R* and *M*, and the bases of Anal and Cubital cells a little clearer; veins brown. Venation: *Rs* a little longer than in *inornata*; R_{2+3+4} relatively short and arcuated, from one-third to about two-thirds longer than R_{2+3}; *m-cu* more than one-third its length beyond the fork of *M*.

Abdomen black, the sternites more pruinose; genital shield black, pruinose.

Holotype, ♀, Emerald Pool, 7,275 ft., June 29, 1941 (*C. P. Alexander*). *Paratopotypes*, Sex?, June 30, 1941; 1 ♀, July 12, 1942 (*C. P. Alexander*).

Pseudolimnophila vidua is most closely related to the more eastern *P. inornata* (Osten Sacken, 1869) which differs in details of coloration, especially the legs, the femora not being blackened as in the present fly. It is probable that both species are more or less closely restricted to boggy (oxylophytic) areas.

Limnophila (*Elaeophila*) *angustior* Alexander, 1919.—Emerald Pool, 7,275 ft., June 30, 1941.

Limnophila (*Phylidorea*) *tepida* Alexander, 1926.—Sylvan Lake, 8,000 ft., June 21, 1941; Northeast Entrance, 7,200 ft., June 24, 1941; Obsidian Creek, 7,300 ft., June 27, 1941; Emerald Pool, 7,275 ft., June 29, 1941. The Sylvan Lake specimens have the entire thorax darker gray and more heavily pruinose than in the type.

Limnophila (*Phylidorea*) *claggi* Alexander, 1930.—Tower Falls, 6,500 ft., June 23, 1941.

Limnophila (Phylidorea) nycteris sp. nov.—General coloration polished black, including the head and the entire disk of the praescutum; fore femora with more than the apical half blackened, the posterior pair narrowly blackened at tips; tibiae and basitarsi brownish yellow, the tips narrowly blackened; wings with a weak brownish tinge, the stigma brown; veins of outer two-thirds of wing conspicuously seamed with pale brown; *Rs* elongate; male hypopygium with the gonapophyses conspicuously bifid at apex.

♂. Length, about 12 mm. ♀. Length, about 14 mm.; wing, 10 mm.

Rostrum and palpi black. Antennae short; scape and pedicel black, flagellum dark brown; basal flagellar segments short-cylindrical, the outer segments more elongate; longest verticils of outer segments a little exceeding the segments in length. Head polished black, strongly prolonged and narrowed behind; anterior vertex relatively wide, nearly three times the diameter of scape.

Pronotum and mesonotum polished black, the extreme lateral borders of praescutum, median area of scutum and the scutellum sparsely gray pruinose. Pleura black, gray pruinose, dorsopleural membrane dusky. Halteres yellow.

Legs with the coxae black, sparsely pruinose; trochanters obscure yellow; femora yellow basally, the tips blackened, very broadly so on fore pair where the outer three-fifths is included, much narrower on the posterior legs where about the distal eighth is blackened; tibiae and basitarsi brownish yellow, the tips narrowly darkened; remainder of tarsi black. Wings (Fig. 16)) with a weak brownish tinge, the prearcular field and cells *C* and *Sc* yellow; stigma oval, brown; narrow but relatively conspicuous pale brown seams on most of the longitudinal veins, most conspicuous and distinct on the outer two-thirds of wing, the wing tip somewhat similarly darkened; veins brown, yellow in the flavous portions. Venation: *Rs* relatively long, angulated and spurred at origin, nearly three times as long as R_{2+3+4}; *m* reduced in length to lacking (as shown).

Abdomen, including the genitalia of both sexes, black; ovipositor with the elongate cerci horn-yellow. Male hypopygium (Fig. 19) with the posterior border of tergite, *9t*, gently emarginate. Basistyle, *b*, short and stout, at apex produced into a stout black lobe. Outer dististyle, *od*, a slender rod, gradually narrowed and curved to a simple acute black point. Inner dististyle shorter and stouter, simple, provided with numerous erect setae. Gonapophyses, *g*, appearing as flattened plates, each deeply bifid at apex, the outer point longer. Aedeagus slender, weakly emarginate at apex.

Holotype, ♂, Emerald Pool, 7,275 ft., June 30, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, with the type.

The most similar species is *Limnophila* (*Phylidorea*) *euxesta* Alexander (Washington, Oregon) which has the praescutal interspaces conspicuously yellowish gray pruinose to isolate four polished black stripes. It further shows marked differences in the pattern of the legs and wings and in the venation. The unique male specimen of this new fly was found alive in my net while sweeping but both wings had been broken off close to the body.

Pilaria phaeonota sp. nov. Head gray; mesonotum uniformly brownish dark brown, the lateral portions of praescutum brownish yellow; thoracic pleura obscure yellow, weakly patterned with darker; legs obscure yellow, the tips of femora weakly darkened; all tarsi white; wings with a brownish tinge, the long-oval stigma pale brown, a little darker than the ground; R_{2+3+4} shorter than the basal section of R_5; *m-cu* lying far distad, only about one-fourth to one-fifth its length from the fork of M_{3+4}.

♀. Length, about 6.5-7 mm.; wing, 6.5-7 mm.; antenna, about 1.8-1.9 mm.

Rostrum brownish yellow; palpi brown. Antennae of moderate length, with indications that in the male sex it may be elongate; scape and pedicel yellow, flagellum brownish black; flagellar segments long-oval or with the ventral face slightly more protuberant than the upper one; longest verticils from one-third to one-half longer than the segments; terminal segment subequal in length to the penultimate. Head dark brownish gray; anterior vertex broad, five or six times as wide as the diameter of scape.

Pronotum brownish yellow, a little darker above. Mesonotum chiefly dark brown, the median region of scutum very restrictedly paler; humeral and lateral portions of praescutum obscure brownish yellow. Pleura obscure yellow, weakly patterned with brown on the ventral anepisternum and sternopleurite. Halteres with stem yellow, knob dark brown. Legs with the coxae and trochanters pale yellow; femora obscure yellow, the tips weakly darkened; tibiae brownish white, the tips very narrowly darkened; all tarsi white, only the extreme apex of the last segment more darkened. Wings (Fig. 17) with a brownish tinge, the costal and prearcular fields a trifle more yellow; stigma long-oval, pale brown, a little darker than the ground; veins pale brown, including those in the brightened fields. Macrotrichia of veins abundant and of moderate length. Venation: Sc_1 ending opposite or shortly before the level of the fork of *Rs*, Sc_2 a short distance from its tip; R_{2+3+4} shorter than the basal section of R_5; R_{2+3} gently sinuous underneath the stigma; cell M_1 about twice its petiole; *m-cu* lying far distad, only about one-fourth to one-fifth its own length from the fork of M_{3+4}.

Abdominal tergites dark brown, the sternites a trifle paler, the segments with conspicuous yellow setae. Ovipositor with valves slender especially the cerci which are slightly upcurved.

Holotype, ♀, Emerald Pool, 7,400 ft., along small mountain stream on mountainside above the pool, July 12, 1942 (*C. P. Alexander*). *Paratopotype*, 1 ♀.

This very distinct fly is apparently related to a group of eastern Nearctic species centering about *Limnophila albipes* Leonard, 1913, and *L. niveitarsis* Osten Sacken, 1869. All such species have only the posterior tarsi white whereas in the present fly all the tarsi are conspicuously whitened, whence the specific name. I secured the type specimens by sweeping alpine firs along the mountain torrent above mentioned.

Shannonomyia oslari (Alexander, 1916).—Northeast Entrance, 7,200 ft., June 24 and 26, 1941; Emerald Pool, 7,275 ft., June 29, 1941.

Pilaria phaeonota sp. nov.—Head gray; mesonotum uniformly brownish black to black, contrasting abruptly with the yellow pleura and pleurotergite; antennae short in both sexes; wings with a weak brown tinge, the stigma a trifle darker; cell M_1 present, longer than its petiole; abdominal tergites brownish black, basal sternites obscure yellow, narrowly bordered laterally with brown; outer segments, including hypopygium, black.

♂. Length, about 6.5-7 mm.; wing, 8.5-9 mm.; antenna, about 1.2-1.3 mm.

♀. Length, about 10 mm.; wing, 10 mm.

Rostrum and palpi black. Antennae black throughout, short in both sexes. Head dark gray; anterior vertex (male) relatively narrow, about twice the diameter of scape; in female wider, approximately three times the diameter of scape.

Pronotum restrictedly infuscated above, the scutellum and broad lateral portions of scutum yellow. Mesonotum brownish black to black, the surface sparsely pruinose; humeral and lateral portions of praescutum yellow. Pleura and pleurotergite abruptly light yellow. Halteres with stem obscure yellow, brighter at base, knob infuscated. Legs with coxae and trochanters yellow; femora, tibiae and basitarsi obscure yellow, the tips narrowly infuscated; outer tarsal segments uniformly brownish black. Wings (Fig. 18) with a weak brown tinge, the stigma a trifle darker; veins brown. Stigmal trichia relatively numerous. Venation: *Sc* relatively short, Sc_1 ending a short distance before fork of *Rs*, Sc_2 longer, still closer to this fork; *Rs* long, lying relatively close to R_1; R_2 shorter than R_{2+3}; cell M_1 present, longer than its petiole; *m-cu* at or just beyond midlength of cell *1st* M_2; cell *2nd A* relatively narrow.

Abdominal tergites dark brown to brownish black, the basal sternites obscure yellow, with narrow lateral brown borders; outer segments, including hypopygium, brownish black to black. Male hypopygium (Fig. 20) with the outer dististyle, *od*, microscopically serrulate on lower margin just before the apical spine. Inner dististyle darkened, terminating in two powerful bristles.

Holotype, ♂, Elk Park, 7,000 ft., June 28, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotype*, ♂ ♀; *paratype*, 1 ♂, Old Faithful Basin, 7,300 ft., June 30, 1941.

In its general appearance, *Pilaria phaeonota* much resembles the eastern and northern North American *P. tenuipes* (Say), which differs conspicuously in the elongate male antennae. The other western North American species of *Pilaria* having short antennae are quite different in body coloration.

Hexatoma (*Eriocera*) *eriophora* (Williston, 1893).—Yellowstone, without more accurate data, July 23, 1930 (Amer. Mus. Nat. Hist., No. F. 300, 723).

ERIOPTERINI

Gonomyia (Idiocera) proserpina sp. nov. — Belongs to the *blanda* group; general coloration gray, the praescutum with two intermediate brown stripes; antennae and rostrum black throughout; knobs of halteres weakly darkened; wings grayish subhyaline, restrictedly patterned with brown, as in the group; *Sc* long, veins R_{1+2} and R_3 confluent at wing margin; *m-cu* more than its own length before the fork of *M;* male hypopygium with the outer lobe of basistyle blunt at tip; outer dististyle entirely blackened, profoundly split into two acutely pointed arms, the inner one with a lateral spine; aedeagus terminating in a short recurved point.

♂. Length, about 5-5.5 mm.; wing, 6-7 mm.

♀. Length, about 5.5-6 mm.; wing, 6-7 mm.

Rostrum black, sparsely pruinose; palpi black. Antennae black throughout; flagellar segments passing from long-oval to subcylindrical. Head obscure yellow, more pruinose behind; center of vertex with a conspicuous brown spot.

Pronotum yellowish gray, patterned with brown. Mesonotal praescutum gray with two conspicuous intermediate brown stripes that diverge slightly behind, crossing the suture and involving the mesal portions of the scutal lobes; pseudosutural foveae conspicuous, their inner end reaching the dark stripes; scutellum light brownish yellow, somewhat brighter medially; remainder of mesonotum gray. Pleura gray, with a conspicuous obscure yellow longitudinal stripe extending from the fore coxae to the base of abdomen, passing above the base of the hind coxae; dorsopleural membrane weakly darkened. Halteres long, stem yellow, knob weakly darkened. Legs with the coxae chiefly testaceous yellow, their bases narrowly darkened; trochanters obscure yellow; remainder of legs obscure yellow, the tarsi slightly darkened. Wings (Fig. 21)

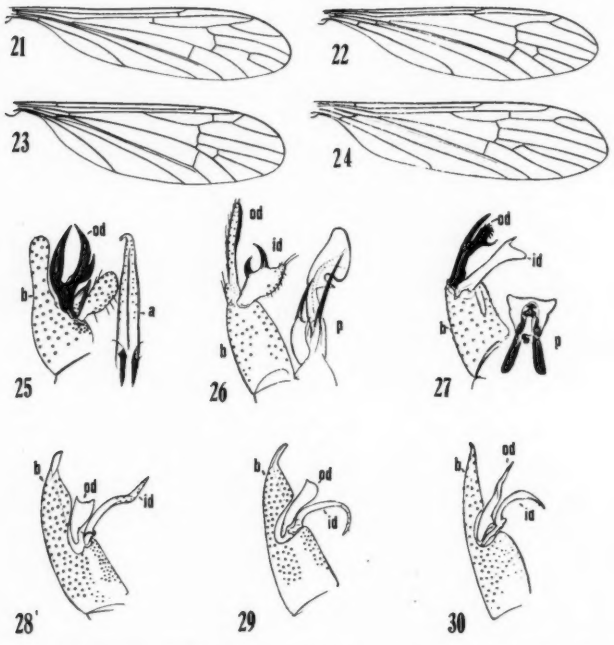


Fig. 21. *Gonomyia (Idiocera) proserpina* sp.n.; venation. Fig. 22. *Gonomyia (Gonomyia) bihamata* sp.n.; venation. Fig. 23. *Erioptera (Gonempeda) yellowstonensis* sp.n.; venation. Fig. 24. *Erioptera (Empeda) tristimonia* sp.n.; venation. Fig. 25. *Gonomyia (Idiocera) proserpina* sp.n.; male hypopygium. Fig. 26. *Gonomyia (Gonomyia) bihamata* sp.n.; male hypopygium. Fig. 27. *Erioptera (Empeda) tristimonia* sp.n.; male hypopygium. Fig. 28. *Erioptera (Gonempeda) yellowstonensis* sp.n.; male hypopygium. Fig. 29. *Erioptera (Gonempeda) burra* Alexander; male hypopygium. Fig. 30. *Erioptera (Gonempeda) nyctops* Alexander; male hypopygium. (Symbols: *a*, aedeagus; *b*, basistyle; *id*, inner dististyle; *od*, outer dististyle; *p*, phallosome.)

grayish subhyaline, restrictedly patterned with brown, as in the group, including areas at arculus; origin of *Rs;* fork of *Sc;* stigma; along cord; fork of M_{1+2}, and the outer radial field in cells R_3 and R_4; veins brown. Venation: *Sc* relatively long, Sc_1 ending shortly beyond midlength of *Rs*, Sc_2 near its tip; *Rs* long, angulated and spurred at origin; veins R_{1+2} and R_3 confluent at margin, closing cell R_1; *m-cu* more than its own length before the fork of *M*.

Abdomen dark brown, including the hypopygium, the posterior and lateral borders of the tergites narrowly yellow. Male hypopygium (Fig. 25) with the outer lobe of basistyle, *b*, pale, its tip obtuse, with setae throughout the length. Outer dististyle, *od*, entirely blackened, profoundly bifid into two pincer-like arms, the outer one simple, terminating in an acute black point; inner arm of approximately similar shape, its tip acute, on inner margin at near midlength bearing a subappressed lateral spine; apex of main stem just at fork with several microscopic setulae. Inner dististyle a pale yellow compressed blade, the apex subtruncate to obtuse, the surface provided with numerous coarse setae; at base of style with a further flattened blade or edge that terminates in a narrowly triangular chitinized point. Aedeagus, *a*, elongate, relatively narrow, pale throughout, the apex a short recurved point; surface with many setae, especially on margin and on distal half.

Holotype, ♂, Emerald Pool, 7,275 ft., June 30, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, with the type. *Paratopotypes*, 10 ♂ ♀, with the types.

Gonomyia (*Idiocera*) *proserpina* is quite different from all other members of the *blanda* (*sexguttata*) group, especially in the structure of the male hypopygium, as the outer lobe of the basistyle and the pincer-like nature of the outer dististyle. The fly was not uncommon on low vegetation along the small woodland stream at Emerald Pool, especially in the *Ledum* area.

Gonomyia (*Idiocera*) *coloradica* Alexander, 1920.—Old Faithful Geyser, 7,300 ft., June 30, 1941; Emerald Pool, 7,275 ft., June 30, 1941.

Gonomyia (Gonomyia) bihamata sp. nov. — Allied to *extensivena;* rostrum obscure brownish yellow; antennae black throughout, relatively long; head dark gray; scutellum extensively obscure yellow; thoracic pleura yellow, patterned with brown on mesepisternum; wings grayish subhyaline, the stigma faintly darkened; *Sc* relatively long, Sc_1 ending a short distance beyond origin of *Rs;* male hypopygium with the inner dististyle bearing two powerful black spines along the caudal border.

♂. Length, about 4.5-5 mm.; wing, 4.6-6.1 mm.

♀. Length, about 5.5-6 mm.; wing, 6-7 mm.

Rostrum obscure brownish yellow; palpi black. Antennae moderately long; scape and pedicel black, the basal flagellar segments a trifle paler, the outer segments passing into black; basal flagellar segments oval, the outer ones passing into elongate-cylindrical. Head dark gray; eyes (male) large, the anterior vertex correspondingly narrowed.

Pronotum bright yellow above, darker laterally; pretergites similarly light yellow. Mesonotal praescutum chiefly covered by confluent brownish gray stripes, the humeral region and broad lateral borders yellow; scutum yellow, the lobes extensively blackened, sparsely pruinose; scutellum obscure yellow, narrowly darkened across the cephalic border, parascutella dark; mediotergite with the central portion dark gray, the marking narrowed behind, the broad lateral margins yellow; pleurotergite yellow. Pleura light yellow, patterned with reddish brown to brown on the anepisternum and ventral sternopleurite. Halteres relatively long, stem pale yellow, knob infuscated. Legs with the coxae and trochanters yellow; remainder of legs brown, the tarsi passing into black. Wings (Fig. 22) grayish subhyaline, the prearcular and costal fields slightly more whitened; stigma very faintly darkened to scarcely indicated; veins dark brown. Venation: Sc_1 ending a short distance beyond origin of *Rs*, in cases to one-fourth or one-fifth the length of the latter, Sc_2 near its tip; R_{2+3+4} arcuated, a little shorter than *Rs;* cell *1st* M_2 closed; *m-cu* unusually variable in position, in cases a short distance before the fork of *M*, in other cases up to one-third its length beyond the fork.

Abdominal tergites dark brown, the lateral tergal borders and the basal sternites more yellowish; outer sternites a little more darkened; hypopygium obscure yellow. Male hypopygium (Fig. 26) with the outer lobe of basistyle, *b*, a small oval pale lobe. Outer dististyle, *od*, long and slender, the distal third to half on mesal face with a glabrous dusky edge or flange, much as in *extensivena*. Inner dististyle, *id*, complex, the caudal portion produced into two powerful curved blackened spines; apex of style a cylindrical lobe that terminates in the usual two fasciculate bristles. Phallosome, *p*, much as in *extensivena*, the aedeagus widely expanded and flaring at apex, subtended by two unequal blackened spines or apophyses.

Holotype, ♂, Emerald Pool, 7,275 ft., June 29, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, 1 ♀, pinned with type; several additional ♂ ♀, June 29-30, 1941; *paratypes*, 1 ♂, Elk Park, 7,000 ft., June 28, 1941; 1 ♂, Northeast Entrance, 7,200 ft., June 26, 1941.

Although closely allied to *Gonomyia* (*Gonomyia*) *extensivena* Alexander, 1943, of the central Rocky Mountain region, the present fly is evidently distinct, differing especially in the structure of the male hypopygium, notably of the inner dististyle which bears two distinct powerful spines instead of the single spinous blade of *extensivena*.

Gonomyia (*Gonomyia*) *flavibasis* Alexander, 1916.—Emerald Pool, 7,275 ft., June 29 and 30, 1941, abundant.

Erioptera (*Mesocyphona*) *distincta* Alexander, 1912. — Gibbon Canyon, Yellowstone, July 22, 1929 (*M. D. Leonard*). This species is closely allied to *E.* (*M.*) *splendida* Alexander, 1913, of Central America, and the records of distribution for the two have been confused.

Erioptera (*Mesocyphona*) *dulcis* Osten Sacken, 1877. — Emerald Pool, 7,275 ft., June 29 and 30, 1941.

Erioptera (*Hoplolabis*) *rainieria* Alexander, 1943.—Emerald Pool, 7,275 ft., in *Ledum glandulosum* association, June 29, 1941.

Erioptera (*Erioptera*) *septemtrionis* Osten Sacken, 1859.—Emerald Pool, 7,275 ft., June 29, 1941.

Erioptera (*Erioptera*) *villosa* Osten Sacken, 1859.—Emerald Pool, 7,275 ft., June 29 and 30, 1941.

Erioptera (*Helobia*) *cana* (Walker, 1848).—Obsidian Creek, 7,300 ft., June 27, 1941; Emerald Pool, 7,275 ft., June 29, 1941.

Erioptera (Gonempeda) yellowstonensis sp. nov.—General coloration of mesonotum light brown, the pleura pale yellow, variegated with pale brown; legs light brown, the outer segments blackened; wings subhyaline, the stigma faintly darkened; male hypopygium with the apical blade of basistyle darkened, the apex cultrate; outer dististyle small, subquadrate, both outer angles more or less produced, the outer one an acute spine; inner dististyle strongly sinuous, blackened.

♂. Length, about 3.2-3.5 mm.; wing, 4.3-4.5 mm.

Rostrum obscure yellow; palpi dark brown. Antennae brownish black; basal segments crowded, the outer ones elongate. Head brownish yellow to pale brown.

Pronotum weakly infuscated above, yellow on sides; scutellum chiefly pale yellow. Mesonotum light brown, very sparsely pruinose; lateral and humeral portions of praescutum pale yellow; posterior sclerites of notum somewhat paler. Pleura pale yellow, variegated with pale brown on anepisternum, ventral sternopleurite and meron; pteropleurite without setae, as in the subgenus. Halteres pale yellow, the apex of knob infuscated. Legs with the coxae and trochanters testaceous yellow; remainder of legs light brown, the outer segments passing into black. Wings (Fig. 23) subhyaline, the stigma faintly darkened; veins pale brownish yellow. Venation: Sc_1 ending about opposite one-third to one-half the length of R_{2+3+4}, Sc_2 nearly opposite the end of *Rs*; R_{2+3+4} shorter than R_{3+4}; vein R_3 oblique, straight, as in the subgenus; *m-cu* beyond the fork of *M*, the distance somewhat variable, in cases up to nearly its own length.

Abdomen pale brown, the hypopygium slightly more yellowish brown. Male hypopygium (Fig. 28) of the general type of the subgenus, that is, the basistyle, *b*, produced into a long flattened glabrous point or blade beyond the point of insertion of the dististyles. Blade of basistyle, *b*, flattened-compressed, the narrow apex cultrate, blackened; setae of basistyle very long and conspicuous, especially those beyond the point of insertion of the dististyles. Outer dististyle, *od*, a small flattened subquadrate blade, the outer apical angle an acute spine, the larger inner apical angle more obtuse. Inner dististyle, *id*, a long strongly sinuous blackened rod that gradually narrows to a subacute apex; distal half with scattered relatively short setae.

Holotype, ♂, Emerald Pool, 7,275 ft., June 30, 1941 (*C. P. Alexander*). *Paratopotype*, 1 ♂, June 29, 1941; *paratypes*, 2 ♂♂, 1 ♀, Obsidian Creek, 7,300 ft., June 27, 1941; 1 ♀, Canyon Camp, 7,800 ft., June 21, 1941.

Erioptera (*Gonempeda*) *yellowstonensis* is quite distinct from the two Nearctic species of the subgenus *Gonempeda* Alexander so far described. The chief features differentiating these various species are found in the structure of the male hypopygium and I have here illustrated the styli for the three species in question. *E.* (*G.*) *burra* Alexander, 1924, is most similar to the present fly; cultrate blade of basistyle (Fig. 29, *b*) and both dististyles pale; outer dististyle, *id*, with the inner apical angle not produced; inner dististyle, *id*, a long sickle-shaped rod (The specimen figured is not the type but is believed to be conspecific). *E.* (*G.*) *nyctops* Alexander, 1916, has the basistyle (Fig. 30, *b*) much more slender, especially beyond the point of insertion of the dististyles; both dististyles elongate, the outer one a long sinuous rod, the tip acute.

Erioptera (Empeda) tristimonia sp. nov.—General coloration blackened, heavily pruinose; antennae black throughout; halteres with yellow knobs; wings with a weak brown tinge, the prearcular field more whitened; stigmal region very faintly darkened; veins R_3 and R_4 generally longitudinal in position, cell R_3 relatively short; cell *1st* M_2 closed; vein *2nd A* straight; male hypopygium with the basistyle not produced caudad beyond the level of origin of the dististyles; outer dististyle blackened, forked, the lateral branch with several slender spines.

♂. Length, about 3.5 mm.; wing, 4.5 mm.; antenna, about 0.8 mm.

♀. Length, about 4 mm.; wing, 5 mm.

Rostrum and palpi black. Antennae black throughout, relatively short; flagellar segments oval, the outer ones becoming more elongate; terminal segment subequal in length to the penultimate and a little stouter; verticils of basal flagellar segments elongate, about twice the length of the segments, of the outer segments about one-half longer than the segments. Head blackish, sparsely pruinose.

Prothorax and mesothorax uniformly blackened, heavily gray pruinose to conceal the ground; pretergites and dorsopleural region darkened. Pleura, including the pteropleurite, without setae. Halteres with stem testaceous, knob yellow. Legs with the coxae gray pruinose; trochanters obscure yellow, the posterior pair darker; femora obscure yellow basally, the tips broadly dark brown; tibiae chiefly yellow, the tips weakly darkened; tarsi obscure yellow, the outer segments blackened; legs without scales among the relatively short sparse setae. Wings (Fig. 24) with a weak brownish tinge, the prearcular and basal costal field more whitened; stigmal region very faintly and indistinctly darkened; veins brown, more yellowish at the wing-base. All longitudinal veins beyond base, excepting Cu_2, with macrotrichia. Venation: *Sc* relatively long, Sc_1 ending about opposite two-thirds the length of *Rs*, Sc_2 about twice its own

length from the tip; *Rs* strongly arcuated; cell R_3 relatively short, the enclosed branches longitudinal in position, R_3 short and sinuous, R_4 nearly straight; R_2 more than its own length beyond the fork of *Rs*, in cases more than twice its length; cell *1st* M_2 closed, *m* much shorter than the basal section of M_3; *m-cu* before the fork of *M;* vein *2nd A* straight.

Abdomen black, heavily gray pruinose; hypopygium black. Ovipositor with valves long and conspicuous, horn-yellow. Male hypopygium (Fig. 27) with both dististyles apical in position, the basistyle, *b*, not conspicuously produced beyond their bases. Outer dististyle, *od*, blackened and heavily sclerotized, conspicuously branched; lateral branch stouter than the axis beyond it, the outer portion with several slender curved spines, with a further single strong spine on the lower outer angle, the space between these spines circular or oval in outline. Inner dististyle, *od*, subequal in size to the outer, entirely pale, the apex an obtuse lobe; on outer margin before tip produced into an acute spine. Phallosomic plate, *p*, slightly expanded outwardly, the outer lateral angles narrowly obtuse to subacute.

Holotype, ♂, Obsidian Creek, 7,300 ft., June 27, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotype*, 1 ♀, pinned with type.

Edwards (Trans. Soc. British Ent., 5: 1-168, 31 figs., with numerous subfigures, 5 pls.; 1938) considers that *Cheilotrichia* Rossi, 1848; *Gonempeda* Alexander, 1924, and *Empeda* Osten Sacken, 1869, represent three subgenera under the oldest name, *Cheilotrichia*. I prefer to consider all three names as representing valid subgenera under *Erioptera* Meigen, 1803. The present fly is closest to *Erioptera* (*Empeda*) *alicia* Alexander, 1914, differing conspicuously in the blackish gray body coloration and in all other details of color. Both of these species have cell *1st* M_2 closed, in this respect agreeing with the typical form of *Cheilotrichia* but it seems advisable to refer these two Nearctic species to *Empeda* rather than to *Cheilotrichia* on the basis of lack of setae on the pteropleura.

Ormosia (*Ormosia*) *garretti* Alexander, 1926. — Sylvan Lake, 8,000 ft., along small mountain stream, June 21, 1941. New to the United States. The normal venation of the species is shown (Fig. 31); one male specimen has cell M_2 of both wings open by the atrophy of *m* (Fig. 32).

Ormosia (Ormosia) opifex sp. nov.—General coloration brown, sparsely pruinose; antennae (male) moderately long, flagellum pale brown; flagellar segments covered with a dense erect pale pubescence, the more proximal segments with very elongate verticils; legs brown; wings grayish subhyaline; cell M_2 open by atrophy of *m;* Anal veins strongly divergent, *2nd A* straight; male hypopygium with the ninth tergite entire, the caudal margin truncate; outer dististyle a sinuous blackened rod; inner dististyle complex, the lateral portion blackened, produced into a spinous horn, the inner blade expanded, yellow, its margin bearing 9 or 10 elongate setae; gonapophyses appearing as two flattened pale blades.

♂. Length, about 4.5-4.7 mm.; wing, 5.2-5.3 mm.; antenna, about 1.5 mm.

Rostrum and palpi brown. Antennae moderately long; scape and pedicel dark brown, flagellum paler brown; flagellar segments somewhat fusiform with truncated ends, covered with a dense erect pale pubescence; the more basal flagellar segments provided with verticils of unusual length, the longest (flagellar segments 3 or 4) nearly four times the length of the segment, on outer segments these verticils shorter and inconspicuous. Head brownish gray.

Pronotum dark brown; anterior lateral pretergites whitened. Mesonotum almost uniformly brown with a restricted gray bloom, not or scarcely patterned. Pleura brown. Halteres yellow throughout. Legs with the coxae pale brown; trochanters yellow; remainder of legs brown. Wings (Fig. 33) grayish subhyaline, the extreme base a trifle more yellow; veins very pale brown, the macro-

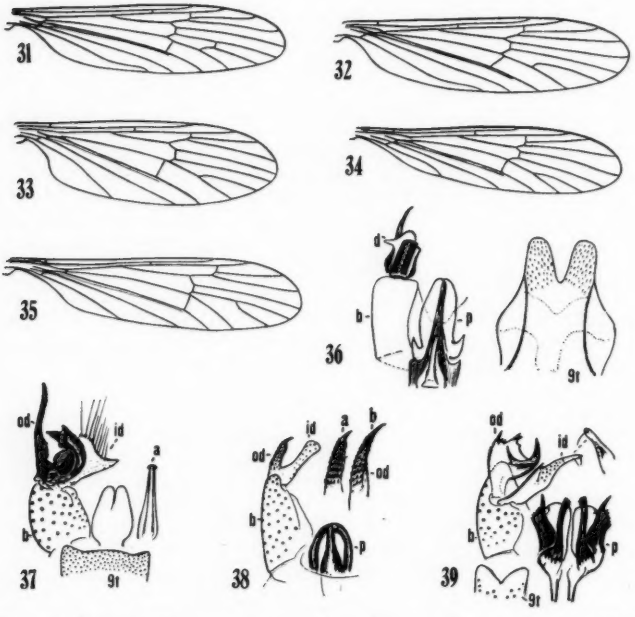


Fig. 31. *Ormosia (Ormosia) garretti* Alexander; normal venation. Fig. 32. The same; abnormal venation. Fig. 33. *Ormosia (Ormosia) opifex* sp.n.; venation. Fig. 34. *Ormosia (Ormosia) absaroka* sp.n.; venation. Fig. 35. *Ormosia (Ormosia) sentis* sp.n.; venation. Fig. 36. *Ormosia (Ormosia) divergens* (Coquillett); male hypopygium. Fig. 37. *Ormosia (Ormosia) opifex* sp.n.; male hypopygium. Fig. 38. *Ormosia (Ormosia) absaroka* sp.n.; male hypopygium. Fig. 39. *Ormosia (Ormosia) sentis* sp.n.; male hypopygium. (Symbols: *a*, aedeagus; *b*, basistyle; *d*, dististyle; *g*, gonapophysis; *id*, inner dististyle; *od*, outer dististyle; *p*, phallosome; *t*, 9th tergite.)

trichia a trifle darker. Macrotrichia abundant and long, well distributed over the wing surface near the wing base. Venation: Cells beyond cord relatively deep; M_2 open by atrophy of *m;* Anal veins divergent, *2nd A* straight on outer two-thirds, the cell wide.

Abdomen, including hypopygium, brown. Male hypopygium (Fig. 39) with the caudal margin of tergite, *9t,* entire, generally truncate or with the central portion gently convex. Outer dististyle, *od,* a sinuous black rod, the basal half stouter, the outer portion slender, its mesal margin and apex slightly roughened. Inner dististyle, *id,* complex in structure, consisting of an outer or lateral more blackened portion that is produced laterad and caudad into a conspicuous spinous horn; inner portion a dilated yellow blade that narrows at apex into a triangular lobe or blade, the outer margin with nine or ten very long pale setae. Gonapophyses appearing as flattened blades, widest across their cephalic portion.

Holotype, ♂, Sylvan Lake, 8,000 ft., June 21, 1941 (*C. P. Alexander*). *Paratopotype,* ♂. Taken along a small mountain stream in the lodgepole pine forest.

The only species with which the present fly requires comparison is *Ormosia* (*Ormosia*) *divergens* (Coquillett, 1905), described from British Columbia. The original description of this latter species is very brief and includes few definite characters. The description of the male hypopygium reads "rather small, the claspers terminate in a curved hook." I am indebted to Dr. Alan Stone of the United States National Museum for making a mount of the male hypopygium of the only male in the type series and sending me a careful drawing of the organ. I have copied this (Fig. 36) in order to compare the species with the present fly. From the drawing it can be seen that the dististyles of the hypopygium, while appearing quite distinct from those of *opifex,* could conceivably be so mounted as to present this different aspect. However, the details of the styli and especially the structure of the ninth tergite, *9t,* show the fly to be a distinct species. The large tergite, with the caudal margin deeply notched, is entirely different from the condition found in *opifex.*

It may be observed that there are several distinct groups in *Ormosia* where cell M_2 is open by the atrophy of *m* rather than the commoner condition of being open by the atrophy of the basal section of vein M_3. These groups include:

1. The *holotricha* group. *O. holotricha* (Osten Sacken, 1859).

2. The *flaveola* group. *O. flaveola* (Coquillett, 1900); *O. absaroka* sp. nov., and several species in Eastern Asia.

3. The *nigripila* group. *O. nigripila* (Osten Sacken, 1869), together with several other species in North America and Eastern Asia.

4. The *divergens* group. *O. divergens* (Coquillett, 1905) and very possibly the present fly.

Ormosia (Ormosia) absaroka sp. nov.—Belongs to the *flaveola* group; general coloration dark brownish gray, including the head and mesonotum; antennae very short, black throughout; halteres yellow; legs dark brown to brownish black, the femoral bases not or scarcely brightened; wings with a brown suffusion, their bases more yellowish; male hypopygium with the outer dististyle strongly roughened by microscopic denticles.

♂. Length, about 4-4.3 mm.; wing, 4.2-5 mm.; antenna, about 0.7-0.75 mm.

♀. Length, about 4.6-5 mm.; wing, 5-5.5 mm.

Rostrum and palpi brownish black. Antennae black, very short in both sexes; basal flagellar segments oval, the outer ones even shorter; verticils about as long as the segments. Head gray; anterior vertex wide.

Thoracic dorsum chiefly dark brownish gray, the sides of the pronotum, lateral pretergites and restricted humeral portions of praescutum more testaceous to yellow; pseudosutural foveae and tuberculate pits black. Pleura dark brown, sparsely pruinose. Halteres yellow, the base of stem restrictedly more darkened. Legs with the coxae and trochanters brown; remainder of legs dark brown to brownish black, the femoral bases not or scarcely brightened. Wings (Fig. 34) with a brown suffusion, the prearcular and costal fields more yellowish; veins and macrotrichia pale brown; veins in the brightened portions of wing more yellowish. Venation: Basal portions of wing narrowed, restricting the cells, cells *2nd A* being unusually narrow; cell M_2 open by atrophy of *m*, cell M_3 relatively deep; *m-cu* at or very close to the fork of *M*.

Abdomen dark brown, the hypopygium obscure yellow. Male hypopygium (Fig. 38) of very simple construction, as in the group. Outer dististyle, *od*, a simple blackened rod that narrows to an acute terminal spine, the outer surface with abundant subappressed microscopic denticles. Inner dististyle longer, pale yellow, the apex a little expanded. Phallosome, *p*, appearing as an unbroken oval sclerotized plate overlain by the stout aedeagus. In the paratype from British Columbia, the outer dististyle is longer and more attenuated (Fig. 38, B); whether this represents a distinct species or subspecies or merely an extreme condition within the limits of the present fly cannot be decided at this time.

Holotype, ♂, Sylvan Lake, Yellowstone, 8,000 ft., June 21, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, with the type. *Paratopotypes* 4 ♂♂, with the types; *paratypes*, 10 ♂♀, Moscow, Idaho, April 19, 1913 (*J. M. Aldrich*, in U. S. N. M.); Terrace, British Columbia, April 15, 1940 (*Mrs. M. E. Clark*); several ♂♀, Twogwotee Pass, Wyoming, 9,650 ft., July 9, 1942 (*C. P. Alexander*).

Named for the Absaroka (Crow) Indians, inhabiting the type locality of the species. The nearest related ally is *Ormosia* (*Ormosia*) *flaveola* (Coquillett, 1900), described from Alaska (June 27, 1899; *Kincaid*). This latter fly differs especially in the yellow coloration of the body, the distinctly longer antennae, and in slight details of structure of the male hypopygium. This structure of the holotype has been mounted and a careful drawing made for me by Dr. Alan Stone, to whom my very deep thanks are extended for many

favors. Other described species in Japan and Corea include *O.* (*O.*) *confluenta* Alexander, 1922, and *O.* (*O.*) *yankovskii* Alexander, 1940.

Ormosia (Ormosia) sentis sp. nov.—Allied to *meigenii;* general coloration dark brownish gray; antennae black throughout, relatively short; longest verticils unilaterally distributed; halteres yellow; legs brown; wings brownish yellow, restrictedly patterned with brown, most evident as a stigmal darkening; cell M_2 open by the atrophy of the basal section of M_3; Anal veins chiefly divergent, *2nd A* very weakly sinuous on its apical portion; male hypygium with the outer dististyle a massive structure provided with several spinous points; both gonapophyses spinous at tips, the inner pair with a semicircle of strong blackened spines near base.

♂. Length, about 3.5-4 mm.; wing, 4-4.8 mm.; antenna, about 1.1 mm.

♀. Length, about 4.5 mm.; wing, 4.5-4.8 mm.

Rostrum brown; palpi black. Antennae relatively short, brownish black throughout; flagellar segments with the longest verticils unilaterally distributed, much longer on the subbasal segments. Head dark gray.

Pronotum brownish gray, the pretergites pale yellow. Mesonotum dark brownish gray; pseudosutural foveae and tuberculate pits black. Pleura brownish gray, the dorsopleural membrane somewhat more buffy. Halteres yellow. Legs with the coxae brownish yellow; trochanters obscure yellow; femora obscure yellow, the tips passing into brownish black; tibiae and tarsi light brown, the outer tarsal segments blackened. Wings (Fig. 35) with a brownish yellow ground, restrictedly patterned with brown, most evident in the unusually distinct stigma; much narrower brown seams at origin of *Rs*, Sc_2 along cord and outer end of cell M_2; a very restricted darkening on apical wing margin, chiefly produced by tiny brown areas at ends of longitudinal veins; prearcular and costal fields a trifle more yellow; veins brown, more yellowish brown in the brightened basal portions. Macrotrichia of cells very pale brown, abundant. Venation: Cell M_2 open by atrophy of basal section of M_3; a more or less distinct spur of a vein jutting basad from point of union of *m* and outer section of M_3; Anal veins chiefly divergent, the extreme tip of *2nd A* a little sinuous but scarcely affecting the widening of cell *1st A* at margin.

Abdomen, including hypopygium, brownish black to black. Male hypopygium (Fig. 39) with the tergite, *9t*, produced medially, its caudal border pale, with a broad V-shaped notch. Basistyle, *b*, at apex produced into a short obtusely rounded lobe. Outer dististyle, *od*, a massive blackened structure provided with several spinous points; outer margin microscopically scabrous; inner spine or horn very powerful; as would be expected in a multispinous structure such as this, there is considerable variation in the number and relative size of the spines. Inner dististyle, *id*, subequal in length to the outer but slender, the basal half broader, the distal portion slender, its tip narrowly obtuse; outer margin at point of narrowing with an acute spinous point. Phallosome, *p*, appearing as flattened blades that are produced into four gona-

pophyses, all with the tips denticulate; outer pair of apophyses broader and flatter, produced at apex into a longer, more spinous portion; inner pair of apophyses chiefly toothed at apex only but with a semicircle of stronger spines near base.

Holotype, ♂, Obsidian Creek, 7,300 ft., June 27, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, June 24, 1941. *Paratopotypes*, 3 ♂♂, June 24-27, 1941; *paratypes*, 1 ♂, 5 ♀♀, Arizona Creek, Grand Teton National Forest, Wyoming, 6,800 ft., July 4, 1942 (*C. P. Alexander*).

The nearest regional ally of the present fly appears to be *Ormosia* (*Ormosia*) *subcornuta* Alexander, 1920, of the Pacific Northwest. This and other generally similar forms that are allied to the eastern Nearctic *O.* (*O.*) *meigenii* (Osten Sacken, 1859), differ conspicuously in the structure of the male hypopygium.

Ormosia (Ormosia) spinifex sp. nov. — Allied to *meigenii;* general coloration dark gray; antennae of moderate length, black throughout; halteres yellow; legs dark brown, the femoral bases obscure yellow; wings with a brownish tinge, the stigma distinct; cell M_2 open by atrophy of basal section of M_3; vein *2nd A* gently sinuous on distal half, cell *1st A* widest at margin; male hypopygium with the dististyle complex, bearing several blackened spinous points; aedeagus slender, terminating in two divergent blackened horns; gonapophyses appearing as flattened blackened blades, at base with a single erect black spine.

♂. Length, about 4.5-5 mm.; wing, 5.5-6 mm.; antenna, about 1.3-1.4 mm.

♀. Length, about 5-5.5 mm.; wing, 6-6.2 mm.

Rostrum dark brown, pruinose; palpi black. Antennae black throughout, of moderate length; flagellar segments long-oval, with a dense white pubescence and conspicuous verticils, the longest of which are unilaterally distributed. Head dark gray.

Pronotum dark brownish gray. Mesonotum chiefly dark gray, the praescutum without stripes, the pretergites restrictedly yellow. Pleura similarly gray, a little brighter immediately in front of wing-root. Halteres uniformly pale yellow. Legs with the coxae and trochanters yellow; remainder of legs dark brown, the femoral bases obscure yellow; outer tarsal segments somewhat more blackened. Wings (Fig. 40) with a brownish tinge, the prearcular and basal costal fields a little more brightened; stigma conspicuous, darker brown; veins brown, a little more yellowish in the basal portions. Macrotrichia of cells distributed over the entire wing. Venation: R_{1+2} variable in position, from a short distance before the fork of R_{2+3} to a corresponding distance beyond the fork; cell M_2 open by atrophy of basal section of M_3; *m-cu* close to fork of *M;* vein *2nd A* gently sinuous on distal half, cell *1st A* widest at the margin.

Abdomen dark brown, including the hypopygium. Male hypopygium (Fig. 44) with the tergal plate, *9t*, gently widened outwardly, the caudal margin

subtruncate, with a small median notch; surface of tergite with abundant short setulae and, on basal half, several unusually long and strong setae. Dististyle, *d*, complex, terminating in an outer blackened spine and a slightly more cephalic flat blackened apical blade; on face of style with a compound blackened structure that terminates in two strong black spinous points, these somewhat variable in length in different specimens; at base of style on mesal face with a small oval pale cushion that may represent a distinct outer dististyle. Aedeagus, *a*, a slender blackened rod that terminates in two divergent slender black horns that are strongly recurved, the apex between these horns with four or five small blackened points. Gonapophyses appearing as narrow flattened black blades, their tips obtuse, near base of each with a single erect black spine.

Holotype, ♂, Northeast Entrance, 7,200 ft., June 26, 1941 (*C. P. Alexander*). *Allotopotypes*, ♀, with the type. *Paratopotypes*, 3 ♂ ♀, June 24-26, 1941; *paratypes* several ♂ ♀, Sylvan Lake, 8,000 ft., June 21, 1941; ♂ ♀, Big Horn Mts., Wyoming, near Steamboat Rock, June 19, 1941 (*C. P. Alexander*).

From the other generally similar regional species that have cell M_2 of wings open by the atrophy of the basal section of M_3 and vein *2nd A* sinuous, the present fly is readily distinguished by the structure of the male hypopygium, notably the dististyles, gonapophyses and aedeagus.

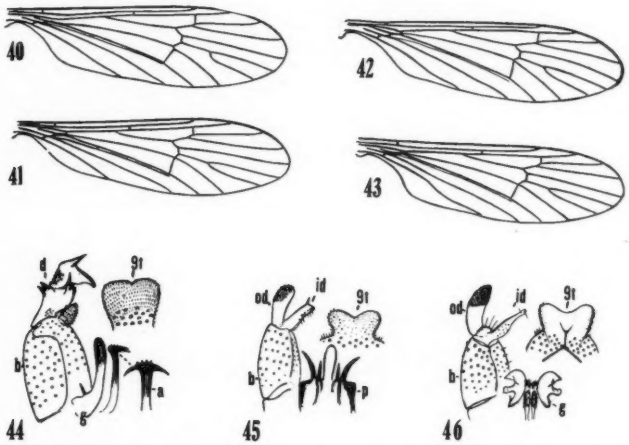


Fig. 40. *Ormosia (Ormosia) spinifex* sp.n.; venation. Fig. 41. *Ormosia (Ormosia) dedita* sp.n.; venation. Fig. 42. *Ormosia (Ormosia) albertensis* Alexander; venation. Fig. 43. *Ormosia (Ormosia) onerosa* sp.n.; venation. Fig. 44. *Ormosia (Ormosia) spinifex* sp.n.; male hypopygium. Fig. 45. *Ormosia (Ormosia) dedita* sp.n.; male hypopygium. Fig. 46. *Ormosia (Ormosia) onerosa* sp.n.; male hypopygium. (Symbols: *a*, aedeagus; *b*, basistyle; *d*, dististyle; *g*, gonapophysis; *id*, inner dististyle; *od*, outer dististyle; *p*, phallosome; *t*, 9th tergite.)

Ormosia (Ormosia) dedita sp. nov. — Belongs to the *similis* group; allied to *adirondacensis;* general coloration dark plumbeous gray; antennae short; halteres yellow; legs dark brown, the femoral bases restrictedly brightened; wings with a brownish tinge, the stigma darker; Anal veins divergent, vein *2nd A* straight; male hypopygium with the inner dististyle bearing a small spine or tooth on outer margin before apex; phallosome consisting of a pale oval blade subtended by two pairs of apophyses terminating in acute blackened spines.

♂. Length, about 4.5-5 mm.; wing, 5-5.6 mm.; antenna, about 0.9-1.0 mm.

Rostrum and palpi black. Antennae short; basal segments black, the outer ones somewhat paler; flagellar segments oval, the longest verticils unilaterally distributed. Head dark gray.

Pronotum brownish black, sparsely pruinose; pretergites restrictedly pale brown. Mesonotum dark plumbeous gray, without evident stripes, the praescutal interspaces indicated by conspicuous yellow setae. Pleura dark plumbeous. Halteres yellow. Legs with the coxae testaceous yellow, the fore pair somewhat darker; trochanters yellow; remainder of legs dark brown, the femoral bases restrictedly brightened. Wings (Fig. 41) with a brownish tinge, the proximal portion of the costal region and the stigma darker brown; veins dark brown. Macrotrichia of cells well-distributed over the entire disk. Venation: Cell M_2 open by atrophy of basal section of M_3; *m-cu* slightly variable in position, in cases close to the fork of *M,* in others a short distance before the fork; Anal veins divergent, vein *2nd A* straight.

Abdomen, including hypopygium, brownish black. Male hypopygium (Fig. 45) with the tergal lobe, *9t,* unusually short and broad, the caudal margin broadly emarginate, the lateral lobes broadly obtuse. Outer dististyle, *od,* long-oval in outline, the distal third provided with about seven rows of appressed spines to completely cover or shingle the apex of style. Inner dististyle, *id,* of approximately the same length as the outer, broadest at base, narrowed on distal half, on outer margin before apex bearing an acute spine, this sometimes reduced to a short stub; lower or mesal portion of style more membranous and provided with several conspicuous punctures that bear setae of moderate length. Phallosome, *p,* consisting of a very pale oval blade, subtended on either side by two pairs of apophyses, the outer pair longer, dilated basally, the acute spinous tips slightly divergent; inner apophyses shorter and straighter, lying nearly parallel to one another.

Holotype, ♂, Northeast Entrance, 7,200 ft., June 26, 1941 (*C. P. Alexander*). *Paratopotypes,* 4 ♂♂.

Ormosia (*Ormosia*) *dedita* has the dististyles of the male hypopygium much like those of *O.* (*O.*) *adirondacensis* Alexander, 1919, and *O.* (*O.*) *brevicalcarata* Alexander, 1927, of eastern North America, but the structure of the phallosome is entirely different.

Ormosia (*Ormosia*) *albertensis* Alexander, 1933. — Northeast Entrance,

June 24, and 26, 1941. Not before recorded from the United States. The wing venation is illustrated (Fig. 42).

Ormosia (Ormosia) onerosa sp. nov. — Belongs to the *similis* group; allied to *mesocera;* mesonotum chiefly brownish black, sparsely pruinose; antennae short in both sexes; wings with a weak brown tinge; vein *2nd A* strongly sinuous; male hypopygium with the inner dististyle unusually slender, dilated on basal half; gonapophyses appearing as flattened blades, their apices acutely pointed, bent laterad.

♂. Length, about 4-4.3 mm.; wing, 4.7-5.2 mm.; antenna, about 1-1.1 mm.

♀. Length, about 4.5 mm.; wing, 5 mm.

Rostrum and palpi black. Antennae short, if bent backward scarcely reaching the wing root, black throughout; basal flagellar segments oval, the outer ones becoming elongate; verticils of the more proximal segments very long, exceeding twice the length of the segments. Head dark gray.

Pronotum obscure brownish yellow to brown; pretergites pale whitish yellow. Mesonotum chiefly brownish black, sparsely pruinose, the humeral and lateral portions of praescutum, dorsal part of pleurotergite and anterolateral portion of mediotergite obscure yellow. Pleura extensively brownish gray, in cases with more or less yellow on the metapleura and dorsal sternopleurite. Halteres weakly darkened, the base of stem paler, the apex of knob whitened. Legs with the coxae and trochanters obscure yellow; femora obscure yellow basally, passing into brown; remainder of legs brown, the outer segments darker. Wings (Fig. 43) with a weak brownish tinge, the stigma slightly darkened; veins and macrotrichia pale brown. Macrotrichia of cells abundant and well-distributed, more sparse to lacking in basal portions of cells *Cu, 1st A* and *2nd A*. Venation: R_2 a short distance beyond fork of R_{2+3+4}; cell M_2 open by atrophy of basal section of M_3; vein *2nd A* strongly sinuous.

Abdomen, including hypopygium, dark brown to brownish black. Male hypopygium (Fig. 46) with the ninth tergite, *9t*, extensive, its caudal lobe broad, gently expanded distally, the caudal margin broadly emarginate. Outer dististyle, *od*, suboval in outline, the distal third or more with parallel rows of long slender black spines. Inner dististyle, *id*, unusually slender, a little dilated on basal half, near apex bearing two long pale setae and with further short setae on the expanded portion. Gonapophyses, *g*, appearing as flattened blades, the outer ends (in slide mounts) bent laterad into broad dusky points, the tip acute.

Holotype, ♂, Northeast Entrance, 7,200 ft., June 26, 1941 (*C. P. Alexander*). *Allotopotype*, ♀, pinned with type. *Paratopotypes*, 1 ♂, pinned with types; 2 additional ♂ ♂, June 24-26, 1941.

Closest to *Ormosia* (*Ormosia*) *mesocera* Alexander, 1917, and *O.* (*O.*) *albertensis* Alexander, 1933, from which it differs in the short antennae in both sexes, the more sinuous vein *2nd A*, and the details of structure of the male hypopygium.

Molophilus (*Molophilus*) *falcatus* Bergroth, 1888.—Emerald Pool, 7,275 ft., June 29, 1941.

Molophilus (*Molophilus*) *colonus* Bergroth, 1888.—Emerald Pool, 7,275 ft., swarming June 29 and 30, 1941.

Molophilus (Molophilus) rostriferus sp. nov.—Belongs to the *gracilis* group, *pubipennis* subgroup; general coloration dark plumbeous gray, without differentiated praescutal stripes; antennae short, black throughout; halteres obscure yellow; legs black throughout; wings with a strong brownish yellow tinge, unpatterned; male hypopygium with both dististyles heavily blackened, the outer one larger, expanded outwardly, its outer margin before apex produced into a blackened spine or point.

♂. Length, about 3.5-4 mm.; wing, 3.5-4.8 mm.; antenna, 1-1.1 mm.

♀. Length, about 4.8-5 mm.; wing, 5 mm.

Rostrum black, sparsely pruinose; palpi black. Antennae short, black throughout; flagellar segments oval. Head dark gray; anterior vertex broad.

Pronotum extensively obscure yellow, darkened medially above; anterior lateral pretergites restrictedly yellow. Mesonotum dark plumbeous gray, without markings; humeral triangle of praescutum more reddish brown; pseudosutural foveae black; apex of scutellum a little reddened. Pleura dark plumbeous gray, the dorsopleural membrane and a spot before the wing root conspicuously yellow. Halteres obscure yellow. Legs with the coxae and trochanters blackened, the former pruinose; remainder of legs uniformly black. Wings (Fig. 47) with a strong brownish yellow tinge, more saturated yellow in the prearcular and costal fields; veins brown, yellow in the more flavous portions. Vena-

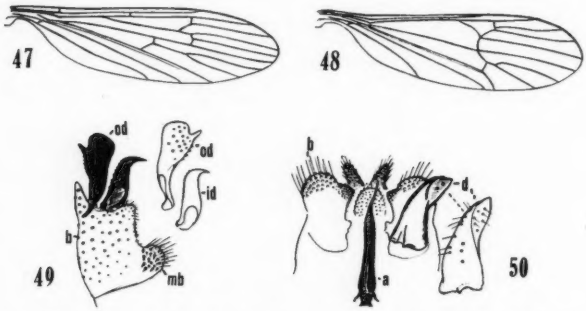


Fig. 47. *Molophilus (Molophilus) rostriferus* sp.n.; venation. Fig. 48. *Cryptolabis (Cryptolabis) molophiloides* sp.n.; venation. Fig. 49. *Molophilus (Molophilus) rostriferus* sp.n.; male hypopygium. Fig. 50. *Cryptolabis (Cryptolabis) molophiloides* sp.n.; male hypopygium. (Symbols: *a*, aedeagus; *b*, basistyle; *id*, inner dististyle; *mb*, mesal lobe of basistyle; *od*, outer dististyle.)

tion: R_2 opposite or just before the level of *r-m;* petiole of cell M_3 nearly three times as long as *m-cu;* vein *2nd A* gently sinuous.

Abdomen, including hypopygium, black. Male hypopygium (Fig. 49) with the outer lobe of basistyle, *b,* relatively small and inconspicuous; mesal lobe, *mb,* large, provided with about 15 blackened spinous pegs, the outer margin of lobe with long delicate pale setae; margin of basistyle distad of the lobe with a few scattered black spines. Both dististyles heavily blackened, the outer, *od,* larger, expanded outwardly, its outer margin before apex produced into a strong blackened spine or point; margin of style basad of this projection with a few microscopic roughenings; disk of style with several scattered microscopic punctures. Inner dististyle, *id,* more slender, the acute tip bent at a right angle to the remainder of style; outer margin usually smooth, in some cases with a few appressed spicules.

Holotype, ♂, Elk Park, 7,000 ft., June 28, 1941 (*C. P. Alexander*). *Allotopotype,* ♀, pinned with type. *Paratopotypes,* 1 ♂, 2 ♀ ♀; *paratypes,* 2 ♂ ♂, 2 ♀ ♀, Upper Falls of the Yellowstone River, 7,500 ft., June 22, 1941; several ♂ ♀, Twogwotee Pass, Grand Teton National Forest, Wyoming, 9,650 ft., July 9, 1942 (*M. M. Alexander*); several ♂ ♀, near Jackson Lake, Wyoming, in a swampy meadow, 6,800 ft., July 5, 1942 (*C. P. Alexander*).

Molophilus (*Molophilus*) *rostriferus* is very different from the other regional members of the *pubipennis* subgroup, differing especially in the dark gray coloration, short black antennae, uniformly black legs, and in the structure of the male hypopygium, especially the outer dististyle with its conspicuous beaklike lateral spine. Among such allied species it is apparently most similar to *M.* (*M.*) *colonus* Bergroth, 1888,, which differs in the patterned wings and in the structure of the male hypopygium.

Cryptolabis (Cryptolabis) molophiloides sp. nov.—General coloration almost uniform brownish black, sparsely pruinose, scutellum more testaceous; thoracic pleura and pleurotergite variegated with obscure yellow; knobs of halteres more or less infuscated; femora pale brown, the tips blackened; wings whitish, restrictedly patterned with darker; wing base more whitened; sparse macrotrichia in outer ends of cells R_4 to M_3, inclusive; *Rs* sinuous, relatively short; *r-m* at or before fork of *Rs;* male hypopygium castaneous; dististyle a flattened blade, its margin almost entire, before apex with a more or less distinct notch.

♂. Length, about 3.5-4 mm.; wing, 4-5 mm.

♀. Length, about 4 mm.; wing, about 5-5.5 mm.

Rostrum and palpi dark brown. Antennae brownish black throughout; flagellar segments oval; verticils relatively long. Head dark brown, sparsely pruinose, especially the front and narrow orbits; anterior vertex (male) moderately wide, about twice the diameter of scape.

Pronotum obscure testaceous yellow. Mesonotum almost uniformly brown-

ish black with a gray pruinosity, the praescutum without stripes; scutellum more testaceous, sparsely pruinose; a more or less distinct yellow area on cephalic portion of mediotergite and pleurotergite. Pleura blackened, sparsely pruinose, with a more or less distinct obscure yellow area on the dorsal sternopleurite; dorsopleural area, including lateral portions of praescutum, obscure yellow. Halteres brownish yellow, the knobs more or less infuscated. Legs with the coxae and trochanters pale brown; femora pale brown, the tips gradually but extensively blackened, most extensively so on fore pairs; tibiae and basitarsi pale brown, their tips narrowly darker brown; remainder of tarsi brownish black. Wings (Fig. 48) whitish subhyaline, very restrictedly patterned with brown, including the small stigma, a narrow seam on anterior cord, and a slight axillary darkening; even less evident seams along vein *Cu* and the longitudinal veins beyond cord; prearcular and costal fields more whitened; veins brown, pale in the whitened areas. Macrotrichia of cells relatively extensive but sparse, including series in cells R_4, R_5, M_2 and M_3; in some individuals these more restricted or even lacking in certain of these cells. Venation: *Rs* relatively short, strongly sinuous; *r-m* at or before the fork of *Rs; m-cu* at or beyond midlength of M_{3+4}; *Rs* in longitudinal alignment with R_5 and *M* often in alignment with M_{1+2}, as figured.

Abdomen brownish black, sparsely pruinose; male genitalia slightly more castaneous. Male hypopygium (Fig. 50) about as shown. Dististyle, *d*, a flattened blade, broad at base, narrowed to the subobtuse or narrowly acute apex, the margin before apex with a more or less distinct notch; surface of style with relatively numerous setae, those of the outer surface larger and somewhat retrorse. Aedeagus, *a*, stout, straight.

Holotype, ♂, Old Faithful Geyser, 7,300 ft., June 30 1941 (*C. P. Alexander*). *Allotopotype*, ♀. *Paratopotypes*, 2 ♂♂, 1 ♀, Emerald Pool, 7,275 ft., June 30, 1941; *paratypes*, 16 ♂♀, Jenny Lake, Grand Teton National Park, 6,800 ft., July 13, 1941 (*C. P. Alexander*); the latter series was taken in dry pine forest near the lake, remote from any stream or similar flowing body of water.

Cryptolabis (*Cryptolabis*) *molophiloides* is most closely related to *C.* (*C.*) *pachyphallus* Alexander, likewise from the north-central Rockies. This latter species differs especially in certain details of structure of the male hypopygium, especially of the dististyle, which is strongly bidentate or bilobed, and with the lobes of the basistyle differently constructed and armed. The specific name of the present fly is an allusion to the general resemblance to certain species of the genus *Molophilus*, particularly *M.* (*M.*) *colonus* Bergroth, with which the present fly was sometimes associated. It is very difficult to distinguish the sexes in this genus, the terminal structures being generally similar and with the details becoming visible only on slide mounts and under high magnification.

Supplementary Notes on Family Names in the Order Araneae

B. J. Kaston

Within a short time after the appearance of my reference list of family names of spiders (1938) I became aware of a number of omissions and errors. In addition to correcting these errors I am including additional names since my paper was written, and also some comments occasioned by the appearance of several important works on the taxonomy of spiders. As in the previous list, names proposed for families having only fossil representatives are not included, the names are arranged in alphabetical order, and for those groups not considered as families by Petrunkevitch an indication is given where possible of their position in his system.* The number of families in Petrunkevitch's system still remains at 62, the erection of a new one in 1939 being balanced by the simultaneous sinking to subfamily status of one previously (1933 and earlier) considered a family. The names proposed by Kishida (1930) were published in a Japanese periodical to which I have not had access, but for the sake of completeness they are here given (though without page references) as cited in the excellent essay on classification by Bristowe (1938). In my original list I had inadvertently overlooked the names introduced by Caporiacco in a preliminary note to a very extensive discussion. The system he proposed (1938) has been followed in a modified form by Gerhardt and Kästner (1937-1938) in their up-to-date treatise.

ACATTYMIDAE Kishida 1930. Lansania, II:
Acattymia L. Koch is in the subfamily Brachybothriinae of the Ctenizidae.

ACTINOPODIDAE Mello-Leitão 1923. Revista do Museo Paulista, XIII:16.
I had erroneously credited this name to Berland 1932.

APHANTOCHILIDAE Thorell 1873.
Although this group had previously been considered of family status by many, including Petrunkevitch, the latter in 1939 sank it to a subfamily within the Thomisidae.

CINIFLONIDAE Blackwall 1841.
Bristowe, in his *Comity of Spiders* (1939), states on page 6 that species now included in the (European) genus *Coelotes* should be transferred to *Amaurobius*, and species now in *Amaurobius* should be transferred to *Ciniflo* Blackwall 1840, a generic name that had previously been reintroduced by F.O.P.-Cambridge. This would necessitate the resumption of the family name Ciniflonidae in place of Amaurobiidae. Apparently C. L. Koch used the name

* Names accepted by Petrunkevitch appear in bold face; others in Roman capitals.

Amaurobius for spiders of different genera in two of his approximately contemporary publications. The usual citation for the genus is 1837 Uebersicht Arachn. Syst., the genotype of which is *Aranea atrox* De Geer (=*fenestralis* Strøm). This is a true cribellate spider of Europe. But Koch also used the name *Amaurobius* in Heft 151 of Herrich-Schaeffer's continuation of Panzer's "Deutschlands Insecten" in association with only *roscidus* and *tigrinus*. According to Bristowe, "though congeneric with *tigrinus* the identity of *roscidus* is uncertain, so *tigrinus* must be selected as the type. *Tigrinus* is a synonym of *atropus* Walck., so *atropus* Walck. [an Agelnid spider of Europe] becomes the type of *Amaurobius*." Bristowe believes that Heft 151 appeared on October 1, 1836, and thus antedates the Uebersicht Arachn. Syst., in which a cribellate spider was placed with the name *Amaurobius*. However, according to the recent investigations of Schenkling (1939), Heft 151 did not appear until 1837, the same year in which the Uebersicht appeared. Until the priority of one or the other publication can be definitely established I believe it is less confusing to retain *Amaurobius* for the cribellate genus, and hence Amaurobiidae for the family name.

CITHAERONIDAE Caporiacco 1937. Zool. Anz., CXVIII:332.
Subfamily in the Zodariidae.

Drassodidae Berland 1932. Les Arachnides, p. 343.

Synonym of Gnaphosidae. For a long time the name Drassidae, proposed by Sundevall in 1833, was used for this family. When it was shown that *Drassus* was a synonym of *Gnaphosa* it became necessary to change the name to Gnaphosidae. This was done by Pocock in 1898. The new name was reluctantly accepted by Simon, but was not used by others, e.g., Petrunkevitch and Berland, who preferred to consider long-standing names like Drassidae as *nomina conservanda*. Simon and Berland had already accepted Salticidae (in place of Attidae) and finally Petrunkevitch (1939) decided likewise. However, he stated that, "the case of *Drassus* is somewhat different. With the change of this name to *Drassodes* there is no valid reason why the family name should be changed to *Gnaphosidae* instead of *Drassodidae*." But I fail to see how this case is different. Just as *Attus* Walckenaer 1805 is a synonym of *Salticus* Latreille 1804, so also is *Drassus* Walckenaer 1805 a synonym of *Gnaphosa* Latreille 1804, and these data are given by Petrunkevitch himself in his Systema Aranearum. The name *Drassus* having thus been changed not to *Drassodes* (which is an entirely different genus) but to *Gnaphosa*, the latter becomes the type genus to the stem of the name of which *idae* is to be added, in accordance with Article 4 of the Rules of Nomenclature.

EPEIRIDAE Sundevall 1833.

This name had long been in common use by American, as well as various European workers and has recently been reintroduced by Chamberlin and Ivie (1942). Simon came to regard *Epeira* as a synonym of *Araneus* [=*Aranea*] and therefore discarded the name Epeiridae. But he disregarded the rules when in 1890 he proposed the name Argiopidae to take its place. Dahl in 1912 pro-

posed Araneidae, which, for one who considers *Epeira* a synonym of *Aranea*, is in acordance with Article 5 of the International Code. But *Epeira* is recognized as valid by Petrunkevitch in his more recent publications, so that the name Epeiridae, having priority, must be used again.

Erigonidae Gerhardt 1923.

In the same paper in which this name was used Gerhardt also used interchangeably with it the name Micryphantidae. The latter name dates from Bertkau 1872. The genus *Micryphantes* was considered unrecognizable by Simon in 1929, and species which had been previously placed in it were by him assigned to his newly erected *Aprolagus* and *Ischnyphantes*. The latter genus is apparently a synonym of *Meioneta* Hull 1920, overlooked by Simon; and Hull, as well as other English and Continental araneologists, still consider *Micryphantes* as a valid name, though there may be some difference of opinion as to what is its type species. Petrunkevitch had accepted the genus in his Systema Aranearum (1928) and had used the name Micryphantidae in 1933. In 1939 for reasons that are not clear he substituted Erigonidae. It seems to me preferable to retain the older name until further light is thrown on this question.

Eusparassidae Caporiacco 1937. Zool. Anz., CXVIII:322.

This name, accepted by Petrunkevitch in 1939, was inadvertently overlooked in my previous list. According to the discussion by Fox (1937) the name *Sparassus* Walckenaer is not invalid although it is by most workers regarded as a synonym of *Eusparassus*. Fox and others continue to use Sparassidae.

HALONOPROCTIDAE Kishida 1930. Lansania, II:

Heptathelidae Petrunkevitch 1939. Trans. Connecticut Acad. Sci. XXXIII: 141.

HEXURIDAE Kishida 1930. Lansania, II:
Subfamily of Dipluridae.

JIKEIDAE Kishida 1930. Lansania, II:

MICROGNATHIDAE Banks 1891. Entom. News, II:84.
Synonym of Oecobiidae.

MYSTARIIDAE Dahl 1913. Vergl. Physiol. u. Morph. d. Spinnentiere, S. 18.
Mystaria Simon is in the subfamily Dietinae of the Thomisidae.

NESTICIDAE Dahl 1926.
Petrunkevitch still considers this group as of subfamily rank, but has moved it from the Theridiidae to the Linyphiidae.

OCYALIDAE Wagner 1894. Mém. Acad. Imp. Sci. Petersburg, XLII:40.
Synonym of Pisauridae.

SASONIDAE Kishida 1930. Lansania, II:
Subfamily of Barychelidae.

THOMISOIDIDAE Mello-Leitão 1941. Ann. Acad. Brasileira Sci., XIII (6): 106.

The genus *Thomisoides* Nicolet has been considered a synonym of *Sicarius* Walckenaer, but Mello-Leitão appears to have shown that Nicolet's name antedates Walckenaer's, and I know of at least two active American araneologists who agree with this conclusion. To this newly erected family belong those spiders with robust, spinose, laterigrade legs. Those with unarmed, slender, prograde legs are left in the Scytodidae *sensu strictu*, this latter name having priority over Sicariidae.

TOXOPIDAE Hickman 1939. Pap. and Proc. Roy. Soc. Tasmania, p. 125.

TRECHALIDAE Simon 1892. Hist. Nat. Ar., I:61.

I had erroneously credited this name to Brown 1898.

REFERENCES

BRISTOWE, W. S. 1938—The Classification of Spiders. Proc. Zool. Soc. London, ser. B., **108**(2):285-322.

———1939—The Comity of Spiders. London. Vol. I, p. 6.

CAPORIACCO, L. DI. 1938—Il sistema degli Araneidi. Arch. Zool. Italiano Tomo **25**, Supplemento Attualità Zoologiche, **4**:35-155.

CHAMBERLIN, R. V. AND W. IVIE. 1942—A hundred new species of American Spiders. Bull. Univ. Utah **32**(13), Biol. Series, **7**(1):61.

FOX, I. 1937—The Nearctic spiders of the Family Heteropodidae. Jour. Washington Acad. Sci. **27**:461-474.

GERHARDT, U. UND A. KÄSTNER. 1937-1938—Araneae. *In* Kükenthal's Handbuch der Zoologie, **3**(2): Lfg. 11 (1937):394-496. Lfg. 12 (1938):497-656.

KASTON, B. J. 1938—Family Names in the Order Araneae. American Midl. Nat. **19**:638-646.

KISHIDA, K. 1930—Lansania **2**:33-43.

PETRUNKEVITCH, A. 1933—An inquiry into the natural classification of spiders based on a study of their internal anatomy. Trans. Connecticut Acad. Sci. **31**:299-389.

———1939—Catalog of American Spiders. Ibid. **33**:133-190.

SCHENKLING, S. 1939—Ueber Herrich-Schaeffer's Fortsetzung zu Panzer, "Faunae Insectorum Germaniae Initia." Jour. Soc. Bibliog. of Nat. Hist. **1**:215-217.

Some Serranid Fishes of Texas,

The Centropomidae, Moronidae and Epinephelidae

J. L. Baughman

Only a single centropomid, *C. undecimalis*, has been found thus far in Texan waters, but it is not unlikely that intensive collecting along the southern portion of our coast would disclose at least one more species of the genus, for the Mexican Servicio de Pesca lists at least six as occurring off the coasts of Tamaulipas. Three species of Moronidae occur in our waters, one of which is much less plentiful than formerly. The Ephinephelids are represented by six genera and ten species.

CENTROPOMUS UNDECIMALIS (Bloch): Snook, pike

First reported by Jordan and Gilbert (1882) from Galveston Bay, or the immediate vicinity, with the comment that it was occasionally caught there during the summer. No such occurrences have been reported in recent years, however, the range of the species rarely extending north of Port Aransas.

Normally a frequenter of the shallow waters of the shore, this fish runs far up brackish and fresh water streams with the incoming tides, in its search for food. However, in company with the tarpon, it can tolerate fresh water, and may even live for extended periods of time in this medium.

For several years numbers of snook were caught in Lake Olmito, near Brownsville, Texas. A freshwater resaca of the Rio Grande, this lake was cut off from communication with the sea by the action of a storm, . . . trapped many snook and tarpon in the lake, where they lived side by side with black bass, and other fresh water forms. Mr. Tate Taylor, of San Benito, says that he first saw pike in the lake in 1935. He caught one of 6½ pounds. Mr. R. B. Sanders, of Harlingen, says that he also caught snook from the lake. Neither has seen any since 1940, when the heavy freeze, noted by Gunter (1941), did such damage to the fish of the coast. Mr. Taylor saw several dead specimens floating on the surface of the lake immediately after the freeze.

Fowler (1931) records a 35-inch female full of roe, from Corpus Christi, taken July 19.

This is one of the important commercial fishes of the Texas coast, large numbers of them finding their way to markets throughout the state. The flesh is white, flaky, and delicate in flavor, and is much relished by everyone familiar with it.

ROCCUS SAXATILIS (Walbaum): Striped bass

The presence of this fish in our waters is uncertain. An old record by Taylor (1878) is headed "The Striped Bass in Texas," but it has not been possible for the writer to examine this paper. More recently, Reed (1941) lists it as one of the important commercial fishes of Texas, but this is manifestly an error.

CHRYSOPERCA INTERRUPTA (Gill): Bar fish

This handsome game fish has become a rare species in Texas waters in recent years, and the only specimen in the Rice Institute collection is one received from Louisiana. In 1892, however, Evermann and Kendall report it from the lower portions of the Trinity and San Jacinto Rivers, from which it was brought in considerable numbers to the Houston markets.

MORONE AMERICANA (Gmelin) White perch

This perch, never previously reported from Texas, was represented in a small collection of fishes from Freeport, forwarded to the Smithsonian Institution. The specimen was identified by Mr. Earl D. Reid.

EPINEPHELUS ADSCENSIONIS (Osbeck): Spotted hind

Not previously reported from Texas, this beautiful little grouper is taken with some frequency on the snapper banks paralleling the Texas coast, and is generally caught in rather deep water by boats fishing for red snapper *Lutianus blackfordi*.

In common with most of the West Indian reef fishes (to which fauna it properly belongs), the spotted hind possesses, to a remarkable degree, the ability to change color, and Townsend (1929) figures four color phases of this fish.

It is an excellent food fish, sometimes found in the Key West markets, occasionally attaining a length of eighteen inches.

EPINEPHELUS STRIATUS (Bloch): Nassau grouper

The only record of this fish is given by Reed (1941), who says that it is rare.

This species, while not as brilliantly colored as the preceding one, exhibits at least eight distinct phases of coloration (Townsend, loc. cit.).

The normal range of *striatus* is the Atlantic coast of tropical America, being found throughout the West Indies, where it is an important food fish, as it is in Florida and Bermuda. These groupers sometimes reach a weight of fifty pounds.

EPINEPHELUS DRUMMONDI-HAYI Good & Bean: Speckled hind, John Paw

Reed (1941) lists the species, giving no locality. Nothing is known of its range in Texas waters.

EPINEPHELUS MORIO (Cuvier & Valenciennes): Red grouper

This is the most common form of the genus throughout the West Indies and about the Florida Keys, where it reaches a length of two or three feet and a weight of 30 or 40 pounds. It is often found in company with red snapper, but, unlike the snappers, *E. morio* does not school. Stearns (1887) has reported young of an inch in length from Pensacola.

In general, this grouper is slower moving than the red snapper and more of a bottom feeder, consuming enormous quantities of crustaceans and smaller fish, while large crabs in almost perfect condition are often found in its stomach (Evermann and Marsh 1900). Longley and Hildebrand (1941) state that it feeds indifferently by day or night, and includes octopuses, shrimp, small stomatopods, and spiny lobsters in its bill of fare.

Like *E. striatus*, *E. morio* is extremely variable in its color, ranging from a light sandy red to so dark a brown as to be almost black.

Reported by Reed (1941), who gives no locality. Freeport fishermen say that it is occasionally taken on the snapper banks.

GARRUPA NIGRITA (Holbrook). Black grouper, warsaw

This gigantic grouper commonly ranges from the south Atlantic and Gulf coasts of the United States to Brazil, and possibly to Sicily (Jordan, Evermann & Clark, 1930). It is reported to reach 500 pounds in weight (Jordan & Eigenmann, 1890).

It is not uncommon on the banks that line the Texas coast, being present throughout the entire year. Its size in these waters rarely exceeds 125 pounds. One of that size, taken at Freeport banks on March 24, 1940, was literally crammed with blue crabs, *Callinectes sapidus*. In all, there was nearly a water pail full of these in the stomach. A 12-pound specimen was taken on the same day, and one of 10 pounds has been caught at Port Aransas.

Schultz (1942) has recently described the young of *Garrupa*, one of his examples being from the Texas Coast. Other young from Massachusetts and Florida indicate a wide breeding range for the species.

This is one of the commercial fishes of Texas.

PROMICROPS ITAIARA (Lichtenstein): Jew fish

This, another giant grouper, is very common about the jetties of the Texas coast. Huge specimens from Port Arthur, Galveston, Freeport, Port Aransas, and Brownsville, all attest its presence in those places, but, in contrast to

Garrupa, it is seldom caught in very deep water. Port Aransas is a particularly favored habitat, and between April 15 and May 28, 1941, at least 40 of these fish were caught there, the greatest number on any one day being 24, weighing from 75 lbs. to 410 lbs., that were caught on May 10th. On May 9th six had been caught, and on April 15th, seven, the smallest weighing 30 lbs., the largest 130 lbs.

Its feeding habits are similar to those of the triple-tail (Breder, 1925).

Spawning occurs in July and August (Schroeder, 1924). Hildebrand (1939) reports an immature specimen, 24 mm. long, and another of 208 mm., in February, from the Gatun locks at Panama.

MYCTOPERCA MICROLEPIS (Goode and Bean): Gag

Specimens of the gag have been taken several times at Freeport and Galveston, while Reed (1941) reports it without giving a locality record. Apparently it is a species confined to the coral reefs; and Longley remarks that he has seen both young and adults among the gorgonians of the Tortugas.

Coloration, as in all groupers, is extremely variable, changing in the same individual from minute to minute.

Goode (1903) states that in Florida this species spawns in June and July, at sea and in the inlets.

MYCTOPERCA FALCATA (Poey): Scamp, bacalao

This fish is closely allied to the foregoing species, and is present in company with both it and the red snapper on the coral reefs of the coast. It is frequently caught on Aransas, Baker, and Hospital reefs at Aransas Pass, and the cast of one, three feet long, that was taken at Freeport, is in the Rice Institute collection.

Its name *falcata* comes from the scythe-like shape of its tail. This species has not been previously recorded from this coast.

PARENEPHELUS ACUTIROSTRIS (Cuvier & Valenciennes): Scirenga

Recently Woods (1942) examined a single specimen (FMNH No. 40260) from the vicinity of Corpus Christi. No further data are available on the species.

as per Schultz, 1939

RYPTICUS SAPONACEUS SAPONACEUS (Bloch & Schneider): Soapfish

Not previously reported from Texas, the single specimen in the Rice collection was taken in a shrimp trawl at Freeport.

REFERENCES

BREDER, CHARLES M., JR. 1925—On the Feeding Behavior of Fishes with Terminal Mouths. Copeia, No. 149: 89-91.

EVERMANN, BARTON WARREN AND WM. CONVERSE KENDALL. 1892—The Fishes of Texas and the Rio Grande Basin considered chiefly with reference to their geographical distribution. Bull. U. S. Fish Comm. **12**:57-126, pls.

EVERMANN, BARTON WARREN AND MILLARD CALEB MARSH. 1900—The Fishes of Porto Rico. Bull. U. S. Fish Comm. **20**(I):49-350, 49 pls., 112 text figs.

FOWLER, HENRY W. 1907—Notes on Serranidae. Proc. Acad. Nat. Sci. Phila. **1907**: 249-258, 5 figs.

———1931—A Collection of Fishes from the Texas Coast. Copeia **1931**(2):46-50.

GOODE, GEORGE BROWN, ET AL. 1903—American Fishes. 2nd ed. rev. by Theo. Gill, Boston, Page & Co., ixvii-562, col. pls. & text figs.

GUNTER, GORDON. 1941—Death of Fishes Due to Cold on the Texas Coast, January, 1940, Ecology **22**:203-208.

HILDEBRAND, S. F. 1939—The Panama Canal as a Passage Way for Fishes, with Lists and Remarks on the Fishes and Invertebrates Observed, Zoologica, **24**(3):15-46, 2 pls.

JORDAN, DAVID STARR, AND C. H. EIGENMANN. 1890—A Review of the Species of Serranidae found in the Waters of America and Europe, Bull. U. S. Fish Comm. **8**:329-442, 10 pls.

JORDAN, DAVID STARR, B. W. EVERMANN AND HOWARD WALTON CLARK. 1930—Check List of the Fishes and Fish-like Vertebrates of North and Middle America north of the Northern Boundary of Venezuela and Colombia. Rept. U. S. Comm. Fish., **1928**(2):1-670.

JORDAN, DAVID STARR, AND CHAS. H. GILBERT. 1882—Notes on Fishes observed about Pensacola, Florida, and Galveston, Texas, with Descriptions of New Species. Proc. U. S. N. M. **5**:241-307.

REED, CLYDE T. 1941—Marine Life in Texas Waters. Tex. Acad. Sci. Pub. Nat. Hist. **2**:xiv-88. num. text figs.

SCHROEDER, WILLIAM C. 1924—Fisheries of Key West and the Clam Industry of Southern Florida, appx. 12. Rept. U. S. Comm. Fish. **1923**:1-74, 29 figs.

SCHULTZ, LEONARD P., AND EARL D. REID. 1942—Descriptive Notes on the Serranid Fish, *Garrupa Nigrita* (Holbrook). Copeia **1942**(1):29-30.

TAYLOR, N. A. 1878—The Striped Bass in Texas. Forest and Stream **2**:7.

TOWNSEND, CHARLES HASKIN. 1928—Records of Changes of Color Among Fishes. Zoologica **9**(9):321-378, 27 col. pls., 12 figs.

WOODS, LOREN P. 1942—Rare Fishes from the Coast of Texas. Copeia **1942**(3): 191-192.

Age Determination in Juvenal Bob-white Quail

George A. Petrides and Ralph B. Nestler

Criteria for separating young of the year from adult gallinaceous birds are comparatively well known and have been treated in an earlier paper (Petrides, 1942), but more exact methods of determining age have yet to be developed for most species. The present study is an attempt to provide age determination data for bob-whites (*Colinus virginianus*) one to five months old, similar to that determined by Louis Bureau for the Hungarian partridge (*Perdix perdix*) and red quail (*Alectoris rufa*) in France. His reports (1911, 1913) contain tables and diagrams of wing feather replacement and growth that purportedly permit the determination of age, within 1 to 3 days, of healthy birds collected during their post-juvenal molt.

In captive quail of these last two species, Bureau says, the post-juvenal wing molt proceeded regularly and simultaneously in all members of a brood, and their feather measurements corresponded precisely with those of wild birds of known age. He describes a change in leg and beak color during December and January for young Hungarian partridges and states that, until the time of mating, young birds possess a weak lower mandible which bends or breaks when the weight of the bird's body is suspended from it. The last criterion of age, he asserts, is the easiest and most practical to use in separating birds of the year from adults.

Unfortunately, the findings for the bob-white are in distinct contrast to those of Bureau in that the much greater individual variation recorded decidedly limits accuracy in age determination, except during the early weeks. Nevertheless, it is believed that the data here presented provide more detailed information on the post-juvenal molt of the bob-white than has heretofore been available. It is hoped that it will prove of some value, at least, in investigations of productivity and in the identification of quail found dead in areas occupied by broods of several ages.

Methods

In accumulating the data here presented, the molting wing feathers of a pair of captive juvenal quail of known age were measured daily from the beginning of the post-juvenal molt until its completion. Additionally, as a check, notes and measurements on the molts of the primaries were made every two weeks on 20 to 35 birds selected at random on each occasion from captivity-reared bob-white quail of the U. S. Fish and Wildlife Service, Patuxent Research Refuge, at Bowie, Maryland. All the birds studied were descendants of at least five generations of captivity-reared quail, originally procured from Virginia and Pennsylvania and have been used in special research work on the nutritive requirements of quail.

They were reared on experimental growing mash until 12 weeks old; were given both the growing mash and a maintenance mash from the sixth week through the twelfth week; and received the maintenance mash solely after the twelfth week. Though consideration must be given the fact that controlled breeding, and regulated feeding of scientifically-balanced diets may have affected the progress of the post-juvenal molt, the authors feel that the data collected offer a valuable basis for further research on the subject.

RECOGNITION OF FIRST YEAR QUAIL

Until the acquisition of adult-type body plumage during the third and fourth months, juvenal bob-whites are easily recognized as such, at first, by their light natal down and, later, by their soft, dark plumage. Stoddard (1931) says that the natal down begins to be replaced at 7 to 9 days of age and that by 14 days, the wing feathers and scapulars "offer considerable protection from light rains"; the tail is then about ¼" long. At three weeks, juvenal plumage predominates, though some down may remain on the head, and the juvenal tail has grown to be about ½" long.

Acquisition of adult-type head, throat, flank, underwing and alula feathers by the specimens studied during the present investigation was well under way by the 70th day. This phase of the post-juvenal molt lasted about 30 days. Stoddard agrees that most young birds appear practically mature at 100 to 111 days.

After this time, birds of the year can be distinguished by their white or buff-tipped greater primary coverts (Van Rossem, 1925) and pointed outer two primaries (Stoddard, *op. cit.*). Adults possess solid gray coverts and rounded outer primaries. The color of the primary coverts is the more reliable character (A. S. Leopold, 1939).

The post-juvenal molt of the bob-white begins well before the juvenal plumage has been completely acquired. Like most gallinaceous birds, this species undergoes an incomplete post-juvenal replacement of feathers in which the outer two juvenal primaries (numbers 9 and 10*), developing late in the autumn, are not replaced until the post-nuptial molt of the following year.

In the captive birds studied, the post-juvenal wing molt began at the distal angle of the wing, with the dropping of primary 1, and proceeded regularly through primaries 1-8. The molt of the secondaries started with the shedding of secondary 3, between the times that primaries 4 and 5 fell. Secondaries 3-9 were then replaced in regular sequence before secondaries 2 and 1 were dropped. The short axial secondary (number 1) was the last remex to be renewed. Bureau found a similar order of molt in the remiges of European quails.

* Remiges are numbered in either direction from the angle of the wing. The short axial feather is secondary 1; the next distal remex is primary 1. Primaries 1-10 and secondaries 1-9 were studied in this investigation.

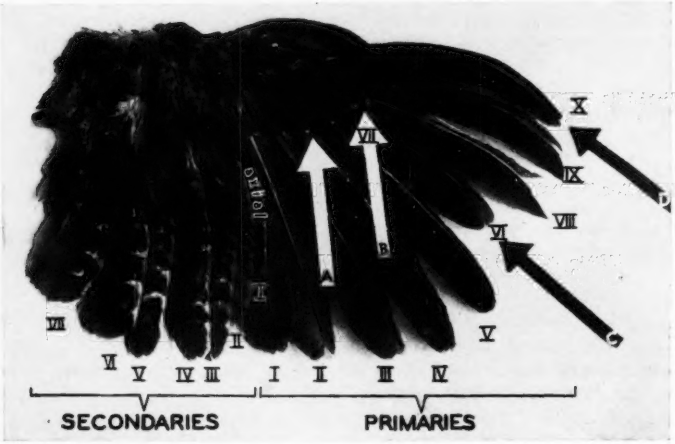


Fig. 1.—Wing of Juvenal Bobwhite 77 days old. The arrows point out (A) the light-colored tips of juvenal greater primary coverts that identify first-year birds; (B) the location of the short, growing quill of the first-winter primary VII, 15 mm. long, hidden by its coverts; (C) the next shortest primary, number VI, 65 mm. long; and (D) the pointed tips of the outer juvenal primaries. The short axial secondary (I) may be seen above primary I. (See Table 3).

TABLE 1.—Ages at which post-juvenal replacement of remiges occurs.

Primaries

	I	II	III	IV	V	
Age when shed	26-30	33-37	40-44	44-50	52-58	
Age when grown	54-58	56-60	60-64	70-76	81-89	DAYS

	VI	VII	VIII	IX	X	
Age when shed	58-62	69-77	97-105	JUVENAL		
Age when grown	99-107	120-128	146-154	58-68	60-70	DAYS

Secondaries

	IX	VIII	VII	VI	V	
Age when shed	100-104	95-98	78-90	74-80	65-70	
Age when grown	131-133	125-132	116-122	108-111	90-95	DAYS

	IV	III	II	Axial	
Age when shed	56-62	48-52	110-113	125-140	
Age when grown	77-88	71-78	138-145	147-162	DAYS

Table 1 indicates the extreme ages at which individual remiges drop and those at which they attain full growth. In all cases, the means lie about midway between the extremes. These data are based principally upon observations of the pair of birds given special study but are modified by records of the control specimens.

In contrast to Bureau's figures of 116 days for the Hungarian partridge and 130 days for the red quail, the bob-white requires 146-154 days to complete the molt of the primaries and 2 to 7 days longer to fully replace the axial secondary.

DETERMINATION OF AGE BY MEASUREMENTS OF THE PRIMARIES

Table 2 presents measurements of the primaries of an average bob-white acquiring its first-winter plumage. Dashes indicate the times at which the juvenal remiges drop. The quills of incoming adult-type wing feathers do not normally project beyond the skin until the second day after shedding. The primaries require about 6 days (and the secondaries 10 to 11 days) to grow long enough to project beyond their greater coverts, and 20 to 50 days to complete their development. For convenience in securing these figures, each wing feather was measured in millimeters from the leading edge of the wing, rather than from the more hidden point of insertion on the trailing edge.

Despite the identical environmental conditions under which they were raised, the extent of variation in the wing molt of birds of the same age was great, as indicated in Table 3 (from which the figures in boldfaced type in Table 2 are taken). It is obvious that deviation from the mean may be so great (7-13 days) after the 10th week that the usefulness of the data for later ages, except in a general way, is decidedly limited.

These measurements are in distinct contrast to Bureau's findings, that each pair of remiges of European quails, drops at exactly regular times and grows with only 1 to 3 days deviation from the average. This regularity permitted him to disregard all measurements except that of the shortest growing feather whose length, up until the next distal remex was replaced, was the principal guide to age. In the bob-white, too, the primaries were found to grow most regularly during their first week or so, but the irregularity of the shedding of the primaries causes this factor to be of little moment; measurement of any growing feather seems to provide equally accurate results in determination of age in this species.

In actual practice, it will be found that some remiges of a bird lag behind the standards set forth in Table 2, while others are in advance of them. Averaging the differences encountered in measuring the outer three growing feathers probably provides as accurate an indication of age as is justified by the variability of other factors. Greatest care must be taken to determine the proper numbers of the growing primaries by counting from the axial secondary (let-

ting this be numbered zero for this purpose) outward, otherwise a missing primary might be overlooked and wrong numbers be assigned to the growing feathers.

The molt of the secondaries is slightly more irregular than that of the primaries.

TAIL MOLT

At 62 days of age, the outermost juvenal rectrices, the first to be dropped, had been replaced by half-grown adult feathers. The other tail feathers were then shed almost *en masse* and, at 116 days, all were as long as their longest upper coverts. The renewed tail was fully grown when the birds were 122 days old.

LEG AND BEAK COLOR

The color of the quails' tarsi varied with age, but the duration of these colors was difficult to determine exactly as the changes were gradual. At 32 days of age, the legs of two captives were pink; at 60 days, straw-colored; and at 83 days, a pale yellow tinged with gray. At the time of writing, these quail are about six months old and retain the yellow-gray leg color. Stoddard (*op. cit.*) states that the legs of adult quail vary in color from yellow-gray to dark gray. He found leg color of no value in age determination in bob-whites more than a few weeks old.

Changes in the color of the beak were not studied, but the bills of birds six months old are identical with those of adults.

LOWER JAW STRENGTH

It is reported that the lower mandible remains cartilaginous in young red grouse, *Lagopus scoticus,* (Committee of Inquiry on Grouse Disease, 1911), sage grouse, *Centrocercus urophasianus,* (Girard, 1937), Hungarian partridges (Bureau, 1911) and red quail (Bureau, 1913) until the birds are about eight months old, and either bends or breaks when the weights of the birds' bodies are suspended from them.

In studying this criterion of age in 18 dead bob-whites ranging in age from 42 to 91 days, it was found that until about 80 days of age, the lower mandibles would flex but not break when the birds were held suspended in mid-air, the thumb and forefinger grasping the lower jaw. Several quail that were 12-13 weeks of age, however, possessed rigid mandibles.

Rigor mortis and freezing prevented successful testing of this criterion in some of the birds studied. Under either of these conditions, the two halves of the bill cleaved together tightly, and had to be pried apart.

TABLE 2.—Average progress of the primary molt in bobwhite quail.

(Measurements are in millimeters; bold faced figures are averages derived from Table 3)

Age (days)	I	II	III	IV	V	VI	VII	VIII	IX	X
28	....									
29	0									
30	15									
31	20									
32	**23**								36	23
33	26								40	26
34	29								43	28
35	33	....							44	29
36	35	0							45	30
37	37	17							46	31
38	**38**	**19**							48	33
39	40	26							50	34
40	43	27							52	35
41	45	30							53	36
42	47	33	....						55	38
43	50	38	0						57	39
44	54	41	16						58	40
45	**58**	**43**	**23**						**59**	**41**
46	64	45	26						62	44
47	66	51	31	....					65	46
48	67	53	37	0					69	50
49	69	59	41	18					70	52
50	71	60	43	25					72	55
51	73	65	50	30					73	58
52	74	70	55	34					74	60
53	75	70	62	37					74	62
54	76	74	63	42	....				75	66
55	77	77	67	46	0				76	66
56	78	80	**69**	**53**	**18**				78	68
57		82	75	55	21				78	69
58		83	77	59	24				79	70
59			79	65	30				79	72
60			81	67	32				81	73
61			82	68	39				83	74
62			84	73	46	....			84	74
63				76	49	0			85	74
64				78	54	15				76
65				80	57	21				77
66				84	61	24				
67				86	64	30				
68				88	67	32				
69				89	69	39				
70				90	**70**	**41**				
71				92	73	46				
72				94	74	49				
73				95	77	54				
74					79	57	....			
75					79	61	0			
76					81	64	13			
77					82	67	16			
78					83	69	20			
79					85	71	25			
80					86	73	30			

TABLE 2.—(Continued)

Age (days)	I	II	III	IV	V	VI	VII	VIII	IX	X
81					90	74	32			
82					92	77	33			
83					93	79	35			
84					94	**80**	**37**			
85					97	81	40			
86						82	43			
87						83	44			
88						83	45			
89						84	47			
90						84	48			
91						85	50			
92						85	52			
93						86	54			
94						86	58			
95						87	59			
96						87	62			
97						88	64			
98						**88**	**68**			
99						91	68			
100						92	70			
101						92	72	....		
102						95	73	0		
103						96	74	12		
104							74	13		
105							75	16		
106							76	20		
107							78	25		
108							79	30		
109							79	32		
110							81	33		
111							83	35		
112							**84**	**39**		
113							85	41		
114							88	43		
115							88	44		
116							89	47		
117							90	50		
118							91	53		
119							92	55		
120							93	56		
121							94	57		
122							95	61		
123							96	64		
124							97	66		
125								68		
126								71		
127								75		
128								**79**		
129								81		
130								83		
131								84		
132								85		
133								87		
134								89		
135								89		

TABLE 2.—(Continued)

Age (days)	I	II	III	IV	V	VI	VII	VIII	IX	X
136								90		
137								92		
138								92		
139								93		
140								93		
141								93		
142								94		
143								94		
144								94		
145								95		
146								95		
147								96		
148								97		
149								97		
150								98		

TABLE 3.—Extent of variation in primary measurements of birds of several ages.

Age (days)	No. of wings Measured	Primary Number	Average Length	Extreme Lengths	Maximum Error in Age Determination
45	10	I	58 mm.	45-65 mm.	
	10	II	43	20-45	
	9	III	23	10-36	4 days
56	19	III	69	61-75	
	19	IV	53	41-67	
	18	V	18	0-36	4 days
70	35	V	70	47-80	
	35	VI	41	0-78	
	7	VII	dropped		
	7	VII	not yet dropped		7 days
84	32	VI	80	52-92	
	32	VII	37	0-60	13 days
98	19	VI	88	82-94	
	20	VII	68	43-85	
	7	VIII	dropped		
	13	VIII	not yet dropped		13 days
112	20	VII	84	80-93	
	20	VIII	39	15-59	9 days
128	20	VIII	79	59-90	8 days

SUMMARY

Following methods described by Louis Bureau (1911, 1913) in France, tabulations were made (1) of the ages at which captivity-reared bob-white quail (*Colinus virginianus*) dropped their juvenal remiges, and (2) the rates at which post-juvenal replacement primaries grew. These were arranged so as to permit the determination of age in healthy birds from one to five months of age. The degree of individual variation was much greater than that found by Bureau, however, and limits accuracy in age determination after the 10th week. The post-juvenal wing molt began on the birds' 28th day and ended when the quail were 146 to 154 days old.

The post-juvenal body molt was found to take place largely between the 70th and 100th days. The juvenal rectrices were renewed from the 62nd to the 122nd days, the new feathers being as long as their longest coverts when the birds were 116 days old. The color of the tarsi varied from pink, at 32 days of age, to straw color at 60 days, and yellow-gray from 83 to 180 days. At six months, the color of the beak was identical with that of adults.

Unlike several other game bird species, the flexibility of the lower jaw was not an accurate index to age in bob-whites older than 11 weeks. Rigor mortis and freezing were found to hinder the testing of this criterion.

ACKNOWLEDGMENTS

The authors wish to thank Arnold Nelson and A. C. Martin of the U. S. Fish and Wildlife Service for their aid in securing study material. The senior author's wife, Miriam Pasma Petrides, deserves special tribute for her daily help in recording feather measurements.

REFERENCES

BUREAU, LOUIS. 1911—L'age des Perdrix: I. La Perdrix grise. Bul. Soc. Sci. Nat. Ouest France (Nantes), sér. 3, **1**(1-2): 124 pp. 35 figs.

———1913—L'age des Perdrix: II. La Perdrix rouge. Bul. Soc. Sci. Nat. Ouest France (Nantes), sér. 3, **3**(2):143 pp. 53 figs.

COMMITTEE OF INQUIRY ON GROUSE DISEASE. 1911—The grouse in health and disease. v. 1, xxiii + 512 pp., 59 pls., 31 figs. Smith, Elder and Co., London (Reviewed in part by Leopold's "Game Management," New York and London, 1933).

GIRARD, GEORGE L. 1937—Life history, habits and food of the sage grouse. Univ. of Wyo. Pub. Sci. **3**(1):1-56.

LEOPOLD, A. STARKER. 1939—Age determination in quail. Journ. Wildlife Management **3**(3):261-265.

PETRIDES, GEORGE A. 1942—Age determination in gallinaceous game birds. Trans. Seventh N. Amer. Wildlife Conference: 308-328.

STODDARD, HERBERT LEE. 1931—The bobwhite quail, its habits, preservation and increase. 559 pp., 69 pls. (part col.), 32 figs. New York.

VAN ROSSEM, ADRIAAN JOSEPH. 1925—Flight feathers as age indicators in *Dendragapus*. Ibis, ser. 12, **1**(2):417-422.

NATIONAL PARK SERVICE,
WASHINGTON, D. C.
AND
PATUXENT RESEARCH REFUGE,
U. S. FISH & WILDLIFE SERVICE,
BOWIE, MARYLAND.

Seasonal Insect Food of the Western Chipping Sparrow[1]

George F. Knowlton and Stephen L. Wood

The following study deals with the recognizable insect food contained in 283 stomachs of the western chipping sparrow, *Spizella passerina arizonae* Coues, collected throughout the state of Utah during the nine years from 1934 to 1942, inclusive. The majority of the birds were collected in areas of Russian-thistle or other host plants of the beet leafhopper, *Eutettix tenellus* (Baker), during late summer and fall, when this insect pest usually is most abundant. The other collections were made throughout the season in agricultural and range areas. The birds were collected as opportunity permitted; this resulted in the collection of: 3 stomachs in April, 7 in May, 10 in June, 14 in July, 45 in August, 174 in September, and 30 in October.

Injurious species of insects contained in the 20 western chipping sparrow stomachs collected from April through June included: seven nymphal and one adult grasshopper; 34 false chinch bugs, *Nysius ericae* (Sch.), 5 Miridae, 2 being *Lygus hesperus* Knt. and 1 *L. elisus* Van D.; 27 leafhoppers, 13 being adult and 1 nymphal *Eutettix tenellus;* 1809 aphids, at least 1528 of these being pea aphids, *Macrosiphum pisi* (Kalt.), 125 *M. coweni* Hunter, 12 *Aphis bonnevillensis* Knlt. and 12 *Epameibaphis atricornis* G.-P.; the beetles included 13 alfalfa weevils, *Phytonomus posticus* (Gyl.), 5 pea weevils, *Bruchus pisorum* (L.), 1 rose snout beetle, *Rhynchites bicolor* Fabr., 1 *Disoncha triangularis* (Say) and other weevils and leaf beetles; approximately half of the lepidopterous larvae were cutworms, many of them being army cutworms and variegated cutworms, only 2 specimens being adult moths; 4 of the Diptera were larvae; 15 ants were contained in 5 stomachs. In addition were 13 spiders and mites, 62 seeds (including Russian-thistle and *Atriplex*) and plant fragments were present in three of the stomachs.

Insect food contained in the 59 stomachs taken during July and August included: 10 adult and 5 nymphal grasshoppers, 1 field cricket, 1 mantid and 1 Mormon cricket egg; 37 termites; 234 adult and 23 nymphal false chinch bugs, 9 Miridae included *Lygus elisus* and *L. hesperus,* 1 *Sinea diadema* (Fabr.), 1 Pentatomidae, 2 Scutelleridae, and also 6 *Geocoris decoratus* Uhl. which big-eyed bug commonly feeds on the beet leafhopper, pea aphid and several other injurious small insects. The leafhoppers included 10 adult and 1 nymphal beet leafhopper contained in the 14 stomachs collected during July and 37 adults and 7 nymphs in the 45 stomachs taken during August; 3 Psyllidae, 2 Cercopidae, 2 Fulgoridae, 23 Coccidae, of the 1424 aphids found, 18 were recognizable as pea aphids, 1 *Lachnus salignus* (Gm.), 2 *Myzus persicae* (Sulz.), 2 *Macrosiphum filifoliae* G.-P., 6 *Aphis cerasifoliae* Fitch, 1 *A. vari-*

1 Contribution from the Department of Entomology, Utah Agricultural Experiment Station, Logan, Utah.

ans Patch, 13 *A. bonnevillensis*, 3 *A. medicaginis* Koch, 2 *A. artemisicola* Wms.; Coleoptera included 7 adults and 5 larval alfalfa weevils, 1 pea weevil (46 weevils of all kinds being found), 2 Elateridae, 1 Scarabaeidae, 1 Dermestidae and 1 Buprestidae; of 26 Lepidoptera only one was adult, 11 being larvae and 14 eggs; Diptera contained 2 Simuliidae, 1 Culicidae, 4 Calliphoridae, 2 Tipulidae and 1 Stratiomyiidae; 104 Hymenoptera were ants. Also present were 5 spiders and mites; 1149 seeds, mostly of weeds, cheat grass and sedge; parasitic nematodes numerous in one of the stomachs; 5 miscellaneous insect eggs also were found.

TABLE 1.—Recognizable insect food in the stomachs of 283 western chipping sparrows; 20 collected April through June, 59 during July and August, and 204 during September and October.

Insect orders	In 20 stomachs April through June	In 59 stomachs July and August	In 204 stomachs Sept. and October	Insect specimens in 283 stomachs totals
Thysanura	0	3	1	4
Collembola	17	19	30	66
Orthoptera	8	19	20	47
Isoptera	0	37	3	40
Neuroptera	0	2	1	3
Odonata	0	1	5	6
Thysanoptera	2	0	2	4
Homoptera	1,838	1,530	3,240	6,608
Hemiptera	53	228	1,139	1,420
Coleoptera	80	149	277	506
Trichoptera	0	0	3	3
Lepidoptera	41	26	92	159
Diptera	5	33	33	71
Hymenoptera	31	131	229	391
Totals	2,075	2,178	5,075	9,328

TABLE 2.—Beet leafhoppers, *Eutettix tenellus* (Baker), which were recognizable in 133 of the 283 western chipping sparrow stomachs examined.

Month	Stomachs containing	*Eutettix tenellus* (Baker) Adult	Nymphs	Total
April	2	2	0	2
May	1	1	0	1
June	4	10	1	11
July	3	10	1	11
August	15	37	7	44
September	93	278	531	809
October	15	56	500	556
Total	133	394	1,040	1,434

TABLE 3.—False chinch bugs, *Nysius ericae* (Schilling), contained in 98 of the 283 stomachs of western chipping sparrows examined during the years 1934 to 1942, inclusive.

Month	Stomachs containing	*Nysius ericae* (Schilling) Adult	Nymphs	Total
April	0	0	0	0
May	3	4	0	4
June	5	30	0	30
July	4	64	4	68
August	14	170	19	189
September	67	561	195	756
October	5	42	0	42
Total	98	871	218	1,089

Among the insects contained in the 204 stomachs collected during September and October were: 20 grasshoppers; 603 adult and 195 nymphal *Nysius ericae* in 72 of the stomachs; 62 *Geocoris decoratus*, 24 *Lygus elisus* in 11 stomachs and 4 *L. hesperus*, 6 Pentatomidae, 2 Ruduviidae, 3 Nabidae and 1 *Orius tristicolor* (Wh.); 334 adult and 1031 nymphal *Eutettix tenullus* in 108 of the 204 stomachs; other leafhoppers included 193 *Thamnotettix geminatus* Van D. and 41 other leafhoppers; a total of 1603 aphids included 405 pea aphids, *Macrosiphum pisi*, 29 *Aphis medicaginis*, 6 *Aphis minuta* G.-P., 10 *Macrosiphum coweni*, 6 *Capitophorus oestlundi* Knlt., 2 *Brevicoryne brassicae* (L.), and 1 *Clavigerus smithiae* (Mon.); 23 coccidae; beetles included 21 weevils, 5 being alfalfa weevils; 2 Scarabaeidae, 1 Coccinellidae, 2 Buprestidae, 2 Tenebrionidae, 1 Melyridae, *Colops bipunctatus* Say, 2 Elateridae, 2 Cicadellidae, 3 Carabidae and 1 Staphylinidae; a large number of the larval Lepidoptera appeared to be cutworms, 7 adult moths and butterflies and 24 eggs also being present; 7 Culicidae, 3 Calliphoridae and 3 Syrphidae flies; 135 ants, 2 Chalcidoidea, 1 Braconidae and 1 Andrenidae were recognized among the 229 Hymenoptera; 6 miscellaneous insect eggs. Also recognizable were 6 spiders, 2818 seeds of weeds and non-grain plants, 15 kernels of wheat.

Occurrence of Upper Canines in Mountain Sheep, Ovis canadensis

Seth B. Benson

Discovery of upper canines or their alveoli in three specimens of mountain sheep led me to search for records of these teeth in sheep and their relatives. Most references concerning the teeth of the Bovidae (antelope, sheep, and cattle) state that upper canines are absent. Actually, exceptions to this rule have been recorded, but they are few. Major (Proc. Zool. Soc. London, 1904, 419-422) reviewed the records previously published and added some new ones. His paper appears to be the most important one on the subject. According to it, upper canine teeth or their alveoli were found in the royal antelope (*Neotragus pygmaeus*), Abyssinian antelope (*Ourebia montana* [=*Ourebia oribi*]), dik-dik (*Madoqua phillipsi*), long-snouted dik-dik (*Madoqua kirkii* [=*Rhynchotragus kirkii*]), springbok (*Antidorcas euchore* [=*Antidorcas marsupialis*]), several unidentified African antelopes, Indian antelope (*Antilope picticauda*), Himalayan goa (*Gazella picticauda*), Saiga antelope [=*Saiga tatarica*], and chamois (*Rupicapra rupicapra*). In most instances the teeth were procumbent, did not cut the gums, and were found in foetal or young animals. Only in *Neotragus pygmaeus* did the teeth ever appear to be functional. Major was of the opinion that, although these rudimentary milk canines were usually functionless and lost early in life, they would be found to be normally present in all foetal and in most very young antelopes. Lönnberg (Arkiv för Zoologi, Stockholm, Band 29 B, no. 1, 1937, 1-3) disagreed with this opinion, since he found no traces of canines in some young and foetal skulls of several kinds of African antelopes and was rather of the opinion that the occurrence of canines in the Cavicornia was only sporadic. He also reported the presence of calcified canines in a young Grant's gazelle (*Gazella granti*) but stated that "it should not have remained very long, because the root shows distinctly that it is beginning to be reabsorbed."

Major referred to the presence of anlagen of upper canines in the embryos of sheep and oxen, but stated that he knew of no occurrence of calcified upper canines in either ovines or bovines. According to Mayo (Bull. Mus. Comp. Zool., 13, 1890, 247-258) in the domestic sheep the dental lamina in the canine region gives rise to an enamel organ which never functions and the entire tooth germ soon disappears. The only reference I found concerning the presence of calcified teeth in sheep was by Kükenthal (Anat. Anz. Jena, 32, 1908, 498-499) who reported calcified and functional upper canines in a week-old domestic sheep. These teeth were small, directed downwards, backwards, and outwards, and were not firmly attached to the jaw. Kükenthal considered them to be milk canines. These teeth differed in position from those found in the antelopes.

It is evident that the presence of upper canines in sheep is a rarity although it is possible that in the literature there are records which I did not find. The presence of these teeth in mountain sheep is therefore of some interest.

Upper canine teeth are present in a specimen of *Ovis canadensis nelsoni*

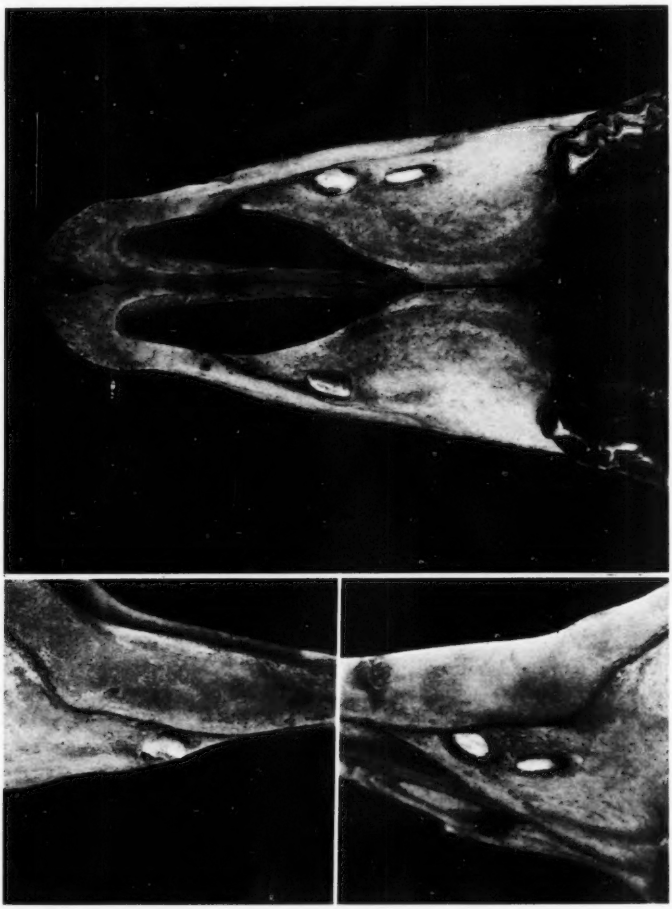


PLATE 1. Upper canines in *Ovis canadensis nelsoni*, M.V.Z. No. 10593. Natural Size. Upper figure, ventral view of palate. Lower left figure, lateral view of right canine. Lower right figure, left canine.

(Mus. Vert. Zool. no. 10593) from the west side of the Colorado River, Imperial County, California, 20 miles north of Picacho, Arizona. The specimen is an adult male in its fifth year (see Plate 1). The permanent dentition is in place and shows wear on all teeth except that the lower canines, apparently retarded in development in comparison with most specimens of equal age, are not yet fully in place. The dentition is also irregular in that the second lower right premolar is absent. The upper canines are asymmetrically placed. The left canine is more exposed than the right canine. Both ends of the left canine are exposed on the lingual side of the maxilla and the middle section is exposed on the nasal side. The tooth is procumbent and did not cut the gums. It is 19 mm. long. It is roughly cylindrical in cross-section in its proximal two-thirds, tapering toward the root. The distal third is widened and flattened on the lower face. Enamel covers the entire surface of the tooth except the lower face so that the canine is similar in structure to the lower incisors and canines. The shaft of the tooth is about 4 mm. in diameter. The flat face is 4½ mm. wide and 7½ mm. long and appears to be composed of dentine. It bears a small low cusp, and the edge, composed of enamel, is slightly crenulate. The anterior, or upper, end of the tooth is smoothly rounded and is composed of enamel. The face of the tooth is almost parallel with the surface of the maxilla and is directed slightly outward. The root has a small concavity which may indicate that growth was not complete.

The right canine is less exposed but projects more above the surface of the maxilla. It has approximately the same shape as the left canine, but the flat face of the tooth is directed slightly inward. The exposed portion is 7½ mm. long, 4½ mm. wide, and 4 mm. deep. The entire tooth is about 20 mm. long as judged from the swelling of the bone covering it. Both of the teeth are slightly curved.

A fully developed left upper canine is present in a specimen of *Ovis canadensis texiana* (no. 110388 U. S. National Museum, Biological Surveys Collection) from the Guadalupe Mountains, Texas. The specimen is a male of five or six years of age. The tooth, directed anteriorly, lies with its long axis parallel to the surface of the surrounding bone. It is partly concealed but the exposed portion is 12½ mm. long and 3½ mm. in diameter. I am indebted to those in charge of the Biological Surveys collection for permission to record this specimen.

Distinct alveoli of canines are present in a weathered skull of an adult male *Ovis canadensis nelsoni* (Mus. Vert. Zool. no. 93097) found on the north side of Potosi Mountain, Clark County, Nevada. Judging from the degree of closure of the cranial sutures, according to the age sequence described by Cowan for mountain sheep (Amer. Midland Nat., 24, 1940, 513-514), the specimen was approximately seven years old. The premaxillae are missing and the most anterior part of the maxillae have been broken off so that the teeth and part of the alveoli are missing. The remaining portion of the alveolus is 12 mm. long and 3 mm. in diameter, indicating that the canine was approximately the

same size as in the other specimen of *O. c. nelsoni*. The teeth were too procumbent to be functional but probably were not entirely concealed by bone.

The most noteworthy features of these canines are their relatively large size, their close resemblance in structure to lower incisors and canines, and the fact that they were present in fully adult specimens. They might represent the canines of the permanent dentition although there is no proof of this, especially in view of the fact that the lower permanent canines do not function until the fourth or fifth year. They have, however, little resemblance to the canines in a weak-old domestic sheep recorded by Kükenthal.

The frequency of occurrence of upper canine teeth in *Ovis canadensis* may be higher than in other ovines or bovines. Of the fifty-three specimens of this species in the Museum of Vertebrate Zoology complete enough for this determination, only two had exposed canines, representing roughly four per cent. Only one was noticed in approximately 250 specimens of *Ovis canadensis* in the collections of the U. S. National Museum and those of the Biological Survey, but I did not examine each specimen carefully for upper canines and kept no record of the number of complete skulls. It is possible that some specimens contain canines entirely buried in the bone. I found no upper canines in eight *Ovis dalli* or in ten *Ovis aries*, or in 61 specimens of various bovines and African antelopes, in the Museum of Vertebrate Zoology collection.

The presence of upper canines in these sheep specimens is an indication of the remarkable persistence in the germ plasm of the factors controlling some structural characters. The fossil record of the Bovidae is limited, but it indicates that the group has lacked upper incisors and canines since the Oligocene.

MUSEUM OF VERTEBRATE ZOOLOGY,
UNIVERSITY OF CALIFORNIA,
BERKELEY, CALIFORNIA.

Swimming, Feeding and Locomotion of a Captive Mole

Charles A. Reed and Thane Riney

Although the behavior of moles in captivity has often been recorded since first reported upon by Godman (American Natural History, vol. 1, 1826), some phases of their activity have not hitherto been noted in sufficient detail. The pattern of the talpid swimming-stroke is of special interest in view of the belief of Campbell (Amer. Jour. Anat., vol. 64, pp. 1-39, 1939) that the "lateral-thrust" digging-stroke of living moles developed from the swimming-stroke of a hypothetical aquatic ancestor.

In May, 1943, there came into our possession a live, male *Scapanus latimanus latimanus*, captured in Berkeley, California. The swimming abilities of this animal were immediately tested.

Many members of the Talpidae are known to be excellent swimmers; indeed *Galemys*, *Desmana*, and *Condylura* are semi-aquatic, but the swimming-stroke has previously been adequately described only for *Neürotrichus* (Dalquest and Orcutt, Amer. Mid. Nat., vol. 27, pp. 387-401, 1942). In this primitive mole the feet of the different sides are used alternately in swimming, a pattern different from the postulated "breast-stroke" of Campbell's hypothetical aquatic ancestor.

When tested in a tub of water of three foot diameter, the swimming-stroke of *Scapanus latimanus* was identical with that of *Neürotrichus*, as recorded by Dalquest and Orcutt. The front feet were held semi-laterally and moved alternately, while the hind feet moved straight fore-and-aft in alternate strokes; the limbs of one side also moved alternately with reference to one another. The fore feet were depressed as much as possible, rather than being extended laterally as in burrowing. The fore foot was brought completely out of the water at the beginning of each stroke. The mole changed direction at will by stopping the action of either fore foot.

The mole swam for six minutes without appearance of fatigue. At first the position of the animal was horizontal with the surface of the water, but as the fur became soaked the hind quarters sank deeper, until after 55 seconds the long axis of the animal made an angle of 70° with the surface of the water and only the snout protruded. Occasionally the hind quarters sank until the animal was vertical or even turned slightly upon its back. In these latter instances the animal always sank and did not regain the surface until it had resumed a more normal position.

This submerged position of the hind quarters of *Scapanus* is in marked contrast to the description of Adams (Mem. and Proc. Manchester Lit. Phil. Soc., vol. 47, no. 4, 39 pp., 1903) of *Talpa europaea*, which swims with head, back, and tail above the surface.

Scapanus at no time dived to escape, as has been reported for *Condylura* in similar circumstances (Schmidt, Jour. Mamm., vol. 12, pp. 99-117, 1931), but

almost constantly swam around the edge of the tub as if seeking a place to climb out. After six minutes an observer's hand was lowered into the water. Upon coming in contact with this platform, the mole immediately crawled upon it and then up the observer's arm. The animal was returned to the water six times, but each time immediately climbed out upon any support offered it and clung to that support when attempts were made to push it off into the water. When dropped into the water, either head-first or tail-first, the animal came to the surface as rapidly as possible.

This mole apparently disliked swimming and made every effort to avoid the water, but it was a sturdy, albeit clumsy, swimmer when forced into water. It is the authors' opinion that the swimming stroke of *Scapanus* and *Neürotrichus* bears no resemblance to the hypothetical "breast-stroke" supposed by Campbell to be ancestral to the digging-stroke of living moles. If our assumption is correct, the moles have always had a simple swimming-stroke, and the peculiar talpid digging-stroke evolved independently. This belief is strengthened by anatomical studies (to be published) of one of us (Reed) on the talpid fore limb.

Aside from an occasional sniffing, no vocal noise was made while the animal was in the water.

Our mole was fed upon earthworms, snails (*Helix aspersa*), and young, freshly-killed rats. At first the latter were eaten in their entirety except for skin, feet, and tail, but after the fourth rat only the viscera were consumed. Snails were not a preferred item and were not eaten if anything else was offered; the mole was never actually observed to eat a snail, but the broken shells and diminished number of them testified as to their fate.

The mole was weighed daily and sometimes oftener; in a period of three weeks the weight varied from 71 to 74 grams. Deprived of all food for 24 hours, its weight fell to 61 grams, but its strength and activity seemed not to be impaired. Offered the carcass of a freshly-killed rat, the mole did not appear particularly hungry and ate leisurely only of the choice items (liver, heart, and spleen). Two hours later its weight was 66 grams. The unfortunate accidental death of the animal a short time later prevented our learning the time necessary for it to recover its normal weight.

The speed of this animal when frightened was two feet per second on a smooth concrete surface. The longest straightaway run was twelve feet, but the animal continued thereafter along the base of a wall at approximately the same rate for twenty-five feet before finding shelter. This speed is four times that recorded by Eadie (Jour. Mamm., vol. 20, pp. 150-173, 1939) for *Parascalops breweri*, but agrees more closely with the speed of 26.7 inches per second reported by Hanawalt (Ohio Jour. Sci., vol. 22, pp. 164-169, 1922) for *Scalopus aquaticus*.

No vocal noise was made by the mole while running; in general it made no noise unless picked up or unless its movements were forcibly constrained; then it produced a rasping squeak.

MUSEUM OF VERTEBRATE ZOOLOGY,
UNIVERSITY OF CALIFORNIA,
BERKELEY, CALIFORNIA.

A New Acanthodian Fish from the Upper Mississippian of Indiana

John W. Wells and Arthur H. Blickle

The large fin spine of an Acanthodian fish to be described below was collected by Miss Dorothy Rothrock, in southern Indiana. The specimen has been deposited in the University of Cincinnati Museum by Dr. F. E. Begthel of Evansville College, Evansville, Indiana.

Genus GYRACANTHUS Agassiz 1837

This organ genus pertains to the fin and free pectoral spines of acanthodian placoderm fishes which are widely distributed in late Paleozoic rocks. Specimens of the best known species, *G. formosus* Agassiz of the Pennsylvanian of Great Britain, may be as much as 40 centimeters in length, indicating fishes of very respectable size, and the specimen dealt with here was probably originally much larger but has lost part of both extremities.

Gyracanthus rothrocki* n. sp.

Figs. 1-6

Description.—Spine, one of free pectoral spines, large and stout, straight, uncompressed, ends not preserved, somewhat flattened towards the base, elongate-triangular in outline, the straight sides forming an angle of about 10°. Inserted portion extending nearly half the present length; angle of insertion about 12°. Upper surface evenly rounded distally, becoming broad and flat basally. Lower surface distally rounded so that the distal cross-section is practically circular; broadly excavated basally by the internal cavity which opens superficially about halfway from the present apical end. The present basal end is about three times as wide as high. Exserted portion highly ornamented above and below by oblique ridges diverging in pairs from the longitudinal mesial line of the upper surface, inclined toward the inserted end, and extending down the sides, where they are more crowded, onto the under surface where they meet, and in some cases, seemingly merge with fine longitudinal striae lying in a slight concavity of the apical under surface. Angle of the ridges and the mesial line about 37°. On the upper surface the ridges are surmounted by elongate transverse enamel tubercles roughly rhomboidal in outline. Basally the tubercles persist down the sides to the limit of the exserted part of the spine, but towards the apex they die out less than halfway down the sides.

* Named for Miss Dorothy Rothrock, the collector of the specimen described.

Occurrence.—Indian Springs shale member, middle Chester formation, Upper Mississippian, a few miles west of Wyandotte Cave, Crawford county, southern Indiana. (One specimen, the holotype, Univ. Cincinnati Mus. No. 23822).

Remarks.—The specimen is well-preserved, but somewhat checked and not wholly free and clean from the shale matrix. It was evidently collected in several pieces, having several transverse fractures, and was repaired by being glued together and washed over with glue. When it came to the hands of the writers it was not considered safe to remove the glue preparatory to removing the remaining shale, for fear the specimen would become even more seriously checked.

Toward the apex there are visible on the sides two sulci crossing the ornamental ridges, and corresponding in position to the present line of insertion. These probably represent earlier lines of insertion of the spine, growth having taken place basally. The angle of insertion indicated by the most distal sulcus is 23°, by the next, 17°, indicating a decrease in the angle of insertion with increasing age and size.

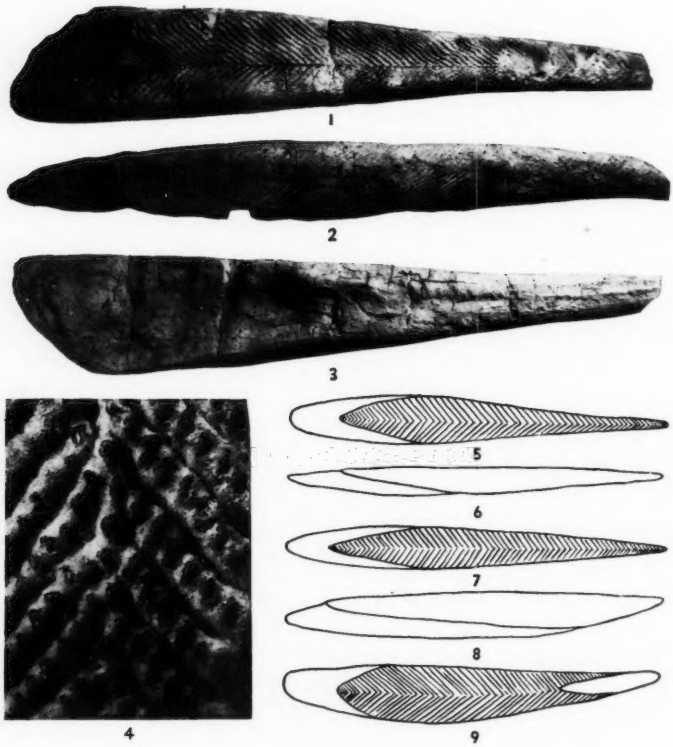
The specimen is not wholly symmetrical in its cross-sectional shape. In the middle part one side (lower side of Fig. 1) is nearly at right angles to the upper surface whereas the opposite side is inclined downwards at about 60 from the surface.

Five other species of this genus have been described from North American Mississippian rocks: *G. alleni* Newberry (1873, p. 331, pl. 37, fig. 3) from the Waverlyan of Ohio, *G. compressus* Newberry 1873, p. 330, pl. 37, figs. 1, 2) from the Waverlyan of Ohio and Indiana, *G. ? cordatus* St. John and Worthen (1883, p. 251, pl. 26, fig. 4) from the Keokuk limestone of Iowa, *G. inornatus* Newberry (1889, p. 177, pl. 23, fig. 5) from the Waverlyan of Ohio, and *G. magnificus* Dawson (1868, p. 210, fig. 55a) from the Mississippian of Nova Scotia. *G. ? cordatus* may not pertain to this genus and is marked by irregular arrangement of the ridge tubercles and a prominent carina along the upper surface. *G. inornatus* is known from very imperfect material, — evidently representing a fin spine with most of the ornamentation removed by abrasion. *G. magnificus* has never been properly described, and the only published figure is a small woodcut. It is a large (55 cm.) spine and may be very similar to *G. rothrocki,* although Dawson's figure suggests that it is arched and compressed.

Of the remaining two species, *G. alleni* and *G. compressus,* the new example is more like the latter but much larger than either. The distribution and arrangement of the ornamentation is similar in *G. compressus* and *G. rothrocki,* but in the former the ridges are proportionally finer. *G. compressus* is known only from fragments, too incomplete to determine the angle of insertion, but sufficient to indicate its most striking character, — the strong lateral compression, which in the middle of the spine seems to have made the thickness at least two and a half times the width. At the same point on *G. roth-*

Dimensions.—

Length	39.5 cm.
Estimated original length	60
Length of inserted portion	18.5
Maximum width, at base of inserted portion	7
Width at distal end	2.5
Maximum thickness, near middle	5
Width, at same point	5.7
Thickness, at distal end	2.5
Number of ridges per 5 cm., upper surface	10
Number of ridges per 5 cm., on sides	15-17
Number of tubercles per 1 cm., on ridges	5



Figs. 1-6. *Gyracanthus rothrocki* n.sp., Chester formation, Indiana. Holotype (U. C. No. 23822). Figs. 1-3, upper, lateral, and lower aspects of spine, ×1/4; Fig. 4, surface ornamentation of mesial portion of upper surface, ×2; Figs. 5, 6, restoration of spine, upper and lateral aspects, ×1/10.

rocki the thickness is a little less than the width. *G. alleni*, known from a nearly complete specimen, is quite different from *G. rothrocki*. It is more compressed, with a subtriangular cross-sectional shape, its angle of insertion is lower (8°), the inserted portion is proportionally much longer, being at least two-thirds the total length, with the result that the lower surface is deeply concave from the exposure of the internal cavity. The ornamentation is similar to that of *G. rothrocki* but the angle of the ridges and the mesial line is greater, being about 47°.

REFERENCES

DAWSON, J. W. 1868—Acadian Geology. 2nd ed., London: xxvi + 694, 231 figs.

NEWBERRY, J. S. 1873—Description of fossil fishes. Geol. Surv. Ohio, Rep. **1**: Geol. and Palaeont., pt. 2, Palaeont., pp. 247-358, pls. 24-40.

———1889—The Paleozoic fishes of North America. U. S. Geol. Surv. Mon. **16**:1-340, 53 pls.

ST. JOHN, O. H., AND A. H. WORTHEN. 1883—Descriptions of fossil fishes. A partial revision of the Cochliodonts and Psammodonts, including notices of miscellaneous materials acquired from the Carboniferous formations of the United States. Geol. Surv. Illinois **7**:55-264, pls. 1-26.

OHIO STATE UNIVERSITY,
COLUMBUS, OHIO
AND
OHIO UNIVERSITY,
ATHENS, OHIO.

Figs. 7, 8. *Gyracanthus alleni* Newberry, Waverlyan, Ohio. Restoration, upper and lateral aspects, about ×1/3.

Fig. 9. *Gyracanthus formosus* Agassiz, Pennsylvanian, Dalkeith, Scotland. Upper aspect, about ×1/7 (after Smith Woodward).

Post-Pleistocene Forest Succession in Northern Idaho[1]

Henry P. Hansen

Introduction

The well drained topography of northern Idaho has limited the number of lakes and ponds affording hydrarch succession and development of peat bogs suitable for pollen analysis. This region was glaciated by several stages of the Pleistocene glaciation. Most of the lakes are large, such as Lake Pend Oreille and Priest Lake, and there has been insufficient organic sedimentation for pollen studies. Most of the smaller lakes that may support the later stages of hydrarch succession on their borders are inaccessible. That part of Idaho north of the Clark Fork River and Lake Pend Oreille is very rugged, the principal mountain ranges being the Selkirk, Cabinet, and Purcell of the northern Rocky Mountain range (Fenneman, 1931). The Selkirks are separated from the other two ranges by the Purcell Trench, which carried a tongue of the Wisconsin ice southward to Lake Pend Oreille (Flint, 1937). The Purcell Trench extends from Lake Pend Oreille to the Kootenai River, and then it carries this stream northward across the International Boundary. The valley floor is covered with fluvio-glacial sediments which are somewhat knolled and kettled. Apparently there has been little modification since the ice melted. The higher peaks of the Selkirk Range to the west reach an elevation of over 7,500 feet, and those of the Cabinet and Purcell Ranges to the east attain altitudes of more than 6,000 feet.

Location and Characteristics of the Bog

The bog of this study is located on the floor of the Purcell Trench, about 2 miles south of the town of Naples and 10 miles south of Bonners Ferry, on the Priest Lake quadrangle, Idaho. It lies in section 13 of T. 60 N., R. 1 W., at an elevation of about 2,000 feet. The bog has apparently been formed in a small, deep kettle pond in the valley floor. The lake occupies an area of about 5 acres, and is surrounded by well-defined zones of hydrophytic vegetation. The innermost zone of a submerged stage is composed chiefly of bladderwort (*Utricularia vulgaris*), water milfoil (*Myriophyllum spicatum*), and stonewort (*Chara* sp.). This sere is followed landward by a floating stage composed of yellow pondlily (*Nymphozanthus polysepalus*) and watershield (*Brasenia schreiberi*). In shallower water near shore is a zone of cattail (*Typha latifolia*) and bulrush (*Scirpus occidentalis*), succeeded shoreward by a sere of cattail, purple marshlocks (*Potentilla palustris*), and sedge (*Cyperus* sp.).

1 Published with the approval of the Monographs Publication Committee, Oregon State College, as research paper No. 76, School of Science, Department of Botany. The expenses of this project were defrayed by a grant-in-aid from the General Research Council, Oregon State College.

On yet higher ground, this is followed by a zone of marshlocks and bog birch (*Betula glandulosa*), while farthest away from open water is a sere composed of birch, willow (*Salix* sp.), and mountain alder (*Alnus tenuifolia*), which in turn grades into the forest on higher ground.

The depth of the peat in the area of sampling is 7.5 meters, and samples were obtained at quarter-meter intervals. The peat is underlain with gravel which grades upward into silt and then clay. The clay in turn grades into a whitish-gray peat composed of a high percentage of calcium carbonate, which was assimilated by the alga, stonewort. The white calcareous peat gradually becomes tan and then brown upward in the profile, with an abundance of carbonate present to the 3-meter horizon. The upper 3 meters of peat are fibrous in texture. A stratum of volcanic ash occurs from 5.75 to 5.6 meters, while glass fragments are present upward as high as 5 meters in the profile. Most post-Pleistocene peat profiles in Washington and Idaho contain a layer of volcanic ash, the origin of which may be Glacier Peak in northern Washington. The stratigraphic position of the ash in relation to the depth of the peat is consistent with that of other peat profiles. The ash stratum usually occurs about three-quarters of the way down from the top. The six-inch layer is thicker than that in most bogs, the only other thicker layer being observed at Newman Lake, near Spokane, Washington (Hansen, 1939b), where it is almost one foot. The usual thickness is one or two inches. Where it is thicker, the ash was probably carried into the pond or lake by incoming streams.

In the preparation of the peat for microscopic analysis, the usual potassium hydrate method was used. In order to eliminate the calcium carbonate assimilated by the alga, stonewort, concentrated nitric acid was added drop by drop until there was no evidence of further effervescence. This facilitated much easier and more accurate identification of the pollen, because the carbonate crystals were so abundant as to obscure the pollen grains. From 100 to 200 pollen grains of forest trees were identified from each level. In separating the species of pine pollen, the size range method was employed (Hansen, 1941a).

Forests in Adjacent Areas

The bog is located near the lower edge of the Canadian life zone. It lies within the larch-pine forest, which is designated as a transition forest between the coast and montane climaxes (Weaver and Clements, 1938). This region is also classified as being forested with a western pine forest type (Larsen, 1930). Western white pine (*Pinus monticola*) is one of the principal species in northern Idaho, and often occurs in almost pure stands, although the climax dominants are western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and lowland white fir (*Abies grandis*) (Huberman, 1935). White pine has been able to persist abundantly as a subclimax species due to fire in the past and lumbering in more recent time. If the forest succession is uninterrupted for several centuries, the dominants gain control, and white pine is found only as old, decadent, and diseased individuals sparsely scattered throughout the stand. In the extensive areas of repeated burns, heavy inva-

sions of lodgepole pine (*Pinus contorta*) and western larch (*Larix occidentalus*) occur. These two species do not usually thrive together in the same stand. The former occupies the dry knolls and exposed ridges toward the upper part of the white pine zone, while larch thrives best on north and east exposures where there is a greater abundance of soil moisture (Larsen, 1929). Both lodgepole pine and larch possess characteristics which permit them to invade and thrive in areas denuded by severe and recurring fire. Lodgepole not only reproduces at an extremely early age, but its seeds are retained in the cones for many years until a fire causes them to open and release tremendous quantities of seeds. Lack of competition then causes this species to develop rapidly until more shade-tolerant species regain a foothold. Larch is long-lived and resistant to fire because of its thick bark and less inflammable foliage. Thus, it will survive several fires, and the large trees result in rapid restocking, if the soil is not too warm and dry.

The temporary stands of lodgepole pine and larch are slowly replaced by western white pine and Douglas fir (*Pseudotsuga taxifolia*) if no further fires occur. These two species also invade and thrive after a single fire that destroys the climax forest, or forests of white pine or Douglas fir (Larsen, 1929). After a period during which the forests are undisturbed by fire, the white pine stands mature, but seedlings of this species fail to develop in the shade. The climax dominants in the meantime have invaded and eventually replace the white pine in the absence of further fire. At higher elevations in the Hudsonian zone occur Engelmann spruce (*Picea engelmanni*), whitebark pine (*Pinus albicaulis*), mountain hemlock (*Tsuga mertensiana*), and alpine fir (*Abies lasiocarpa*). At lower elevations on favorable sites western yellow pine (*Pinus ponderosa*) may be found. Broadleaf species in the valley are mountain alder (*Alnus tenuifolia*), cottonwood (*Populus trichocarpa*), aspen (*P. tremuloides*), mountain maple (*Acer glabrum*), and several species of willows.

The bog is located in a climatic province classified as being humid, microthermal, with adequate precipitation at all seasons (Thornthwaite, 1931). The mean annual precipitation in the region forested with the hemlock-cedar-lowland white fir association in northern Idaho ranges from 27 to 44 inches (Larsen, 1930).

Post-Pleistocene Forest Succession

Lodgepole pine is recorded as having been the predominant, pioneer, post-glacial arboreal invader in areas within range of pollen dispersal to the site of the sediments. It shows 77 per cent at the bottom horizon (Fig. 1). Western white pine is the next most abundant forest tree, being represented by 18 per cent of the pollen in the lowest level. Other conifers recorded by 4 per cent or less are western yellow pine, Engelmann spruce, and fir. Lodgepole pine increases upward from the bottom to attain its greatest proportion of 81 per cent at 6.5 meters, and then with several fluctuations it declines to its minimum of 20 per cent at 2.5 meters. With further rather sharp reversals of trend, it generally increases to the surface where it is recorded to 33 per cent.

Western white pine is portrayed as generally increasing upward from the bottom, superseding lodgepole pine at 4.75 meters, and attaining its maximum of 53 per cent at 3.25 meters. It then remains generally constant to the surface with the exception of an abrupt decrease at 1.5 meters. At the uppermost horizon it shows 42 per cent, the greatest of any species recorded. Pollen of western larch, the third species represented by significant proportions, was not observed until 6.25 meters. The pollen profile of this species is marked by two trends of precipitate increase succeeded by abrupt decrease (Fig. 1). It increases from 5 per cent at 4.5 meters to 30 per cent at 3.75 meters, its maximum proportion of the profile, and then decreases to 6 per cent at 3.5 meters. It shows another significant increase from 4 per cent at 1.75 to 24 per cent at 1.5 meters, then it declines to 6 per cent at 1 meter, and is not represented in the upper two horizons.

Fir is the only other conifer represented by its pollen at every level of the profile. Its maximum is 10 per cent at 2.5 meters. Most of the fir pollen is that of lowland white fir, with some from alpine fir which grows at higher elevations. Western yellow pine is represented at most levels, and attains its greatest proportion of 15 per cent at 1.75 meters. Douglas fir played a minor role in postglacial forest succession, and reaches its peak of 12 per cent at the 5.5 meter horizon. Engelmann spruce also was of minor importance in the forest complex during the post-Pleistocene, and records its maximum proportion of 10 per cent at 7.25 meters. Western hemlock and mountain hemlock are only sporadically recorded, and do not exceed 2 per cent at any level. Broadleaf species represented at many levels are alder, birch, and maple.

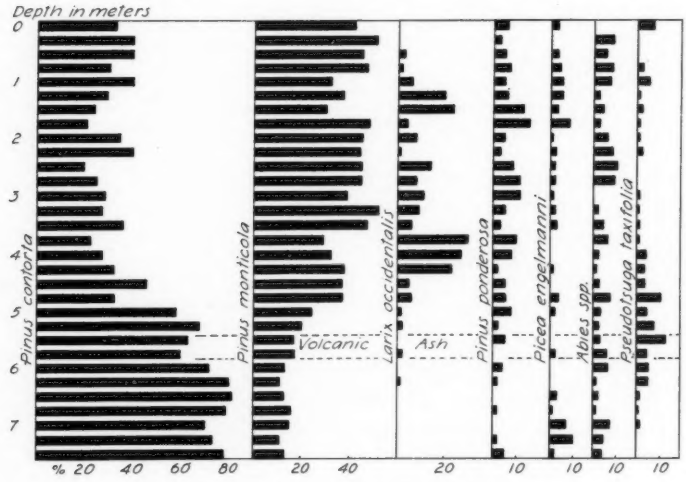


Fig. 1. Pollen profiles, northern Idaho.

Herbaceous species whose pollen is present are grasses, composites, sedges, cattail, and water lily; the last three marking the progress of hydrarch succession. Grasses and composites are so limited in their representation as to offer no significance.

Interpretation of the Pollen Profiles

The predominance of lodgepole pine in the pioneer postglacial forests is consistent with that revealed by pollen analyses of bogs in many other deglaciated areas of the Pacific Northwest (Hansen, 1939a, 1939b, 1940a, 1940b, 1941, 1942, 1943a). The early seed-bearing age of lodgepole and its aggressiveness in invading edaphically disturbed areas were probably responsible for its persistence and mobility under the physiographically unstable conditions that must have existed before an oscillating ice-front. Its decline upward in the profile suggests stabilization of the edaphic and physiographic conditions favorable for the invasion and ecesis of other species. Lodgepole pine could not compete with these species because of its short life span and intolerance for shade. An abundance of western white pine in the pioneer postglacial forests of the Pacific Northwest is also disclosed by pollen profiles from the glaciated region (Hansen, 1939a, 1939b, 1940a, 1941, 1943a). This species reproduces well on mineral soil and being longer-lived and more shade tolerant than lodgepole, it eventually replaces the latter. As white pine is not climax, however, it is also supplanted if forest succession is not interrupted by fire or other factors.

The relative trends of larch and lodgepole and white pine during the time represented from 4.75 to 3.5 meters suggest the occurrence of a series of fires that interrupted forest succession (Fig. 1). The increase of lodgepole pine at 4.5 meters after its rapid decline from its maximum, and the cessation of white pine increase suggest fire that favored an influx of lodgepole pine. Further fire, apparently more extensive and severe, following perhaps within 20 years of the first, favored an invasion of larch that marks the widespread destruction of both lodgepole and white pine. This is portrayed by the maximum of 30 per cent attained by larch at 3.75 meters, where it supersedes both lodgepole and white pine. As these species gradually regained lost ground, larch declined to its previous low proportion, indicating its inability to compete with them as the influence of fire waned. White pine rapidly regained the supremacy it had temporarily lost because of the fires, and remained constant to 1.75 meters. Another series of fires, however, brought about a somewhat similar successional trend of larch and lodgepole and white pine, as recorded from 2.25 to 1 meter. Larch sharply increased to its second highest proportion of 24 per cent at 1.2 meters, while lodgepole and white pine decreased. After the effects of the fires were ameliorated, lodgepole and white pine again increased upward to nearly the surface.

The fact that larch produces a comparatively small amount of pollen, and is therefore under-represented in peat profiles, magnifies the significance of its increase and lends support to the foregoing interpretations. The pollen of western larch occurs in most peat profiles east of the Cascades in Washington

and northern Oregon, but it usually is not present in great enough quantities to depict successional trends. In a montane bog near Bend, Oregon, on the east slope of the Cascades, it is recorded in large enough proportions in the lower levels to denote fire just prior to the beginning of sedimentation (Hansen, 1942). In a subalpine bog in the Blue Mountains of northeastern Oregon, an influx of larch pollen occurs in sufficient proportions to warrant an interpretation of fire as the cause (Hansen, 1943b). It is also recorded as high as 30 per cent in the lower levels of a bog near Spokane, Washington (Hansen, 1939b).

Although western hemlock, western red cedar, and lowland white fir are the chief dominants of the climax forest in northern Idaho, there is no evidence in the pollen profiles for a trend toward the climax. Apparently the hypothetical fires, as reflected by the pollen profiles of larch, white pine, and lodgepole pine, were too severe and extensive for the development of a climax trend in areas within range of pollen dispersal to the site of the sediments. Such a trend, however, is depicted by pollen profiles of another bog in northern Idaho (Hansen, 1939a). This bog is located a few miles west of Priest Lake and about 28 miles west of the bog of this study, in an area with similar floristic and climatic characteristics. In a 12-meter profile, western hemlock, Douglas fir, and lowland white fir are recorded to a total of 47 per cent at 2.5 meters, while white and lodgepole pine show sharp and significant declines. A rapid increase of white pine immediately above suggests a single fire that was not sufficiently severe to permit an invasion by lodgepole pine or larch, although it did interrupt the climax successional trend. Another climax trend is marked by an increase in hemlock in the uppermost levels. Larch is sparsely represented in the profiles, and there were evidently no fires of sufficient magnitude during the postglacial to favor an invasion by this species. White pine superseded lodgepole pine about one meter above the volcanic ash stratum, the same as in this study. There seems to be little evidence for post-Pleistocene climatic trends in the pollen profiles here. Apparently forest succession was largely controlled by competition and the influence of forest fires.

Summary

Pollen profiles of a peat bog in northern Idaho reveal that the predominant, pioneer, postglacial, arborescent invader was lodgepole pine. It was gradually superseded by western white pine early in the profile, the latter remaining generally predominant to the present. Two periods of severe and recurring fires are reflected by the relative trends of western larch and lodgepole and western white pine. A marked increase in the proportions of larch and a decline in those of lodgepole and white pine about one-third up in the profile are indicative of several fires occurring in close succession. Subsequent increase of lodgepole and white pine suggests the amelioration of the effects of the fires and the replacement of larch because of its shade intolerance. A second similar trend of these three species is disclosed higher in the profile, denoting the influence of another series of fires. A final increase of lodgepole

and white pine to the present followed the second influx of larch. The climax forest of this region is composed of western hemlock, western red cedar, and lowland white fir, but there is no evidence in the profiles for a climax trend. Apparently the fires were so severe and occurred so frequently as to prohibit the development of the climax forest. There is no evidence in the pollen profiles for climatic trends.

REFERENCES

FENNEMAN, N. M. 1931—Physiography of western United States. New York.

FLINT, R. F. 1937—Pleistocene drift borders in eastern Washington. Bull., Geol. Soc. Am. **48**:203-232.

HANSEN, H. P. 1939a—Pollen analysis of a bog in northern Idaho. Amer. Jour. Bot. **26**:225-228.

———1939b—Pollen analysis of a bog near Spokane, Washington. Bull. Torrey Bot. Club **66**:215-220.

———1940a—Paleoecology of a montane peat deposit at Bonaparte Lake, Washington. Northwest Science **14**:60-69.

———1940b—Paleoecology of two peat bogs in southwestern British Columbia. Amer. Jour. Bot. **27**:144-149.

———1941—Further pollen studies of post-Pleistocene bogs in the Puget Lowland of Washington. Bull. Torrey Bot. Club **68**:133-148.

———1942—The influence of volcanic eruptions upon post-Pleistocene forest succession in central Oregon. Amer. Jour. Bot. **29**:214-219.

———1943a—A pollen study of two bogs on Orcas Island, of the San Juan Islands, Washington. Bull. Torrey Bot. Club. **70**:236-243.

———1943b—A pollen study of a subalpine bog in the Blue Mountains of northeastern Oregon. Ecology **24**:70-78.

HUBERMANN, M. A. 1935—The role of western white pine in forest succession in northern Idaho. Ecology **16**:137-152.

LARSEN, J. A. 1929—Fires and forest succession in the Bitterroot Mountains of northern Idaho. Ecology **10**:67-76.

———1930—Forest types of the northern Rocky Mountains and their climatic controls. Ecology **11**:631-673.

THORNTHWAITE, C. W. 1931—The climates of North America according to a new classification. Geog. Rev. **21**:633-655.

WEAVER, J. E. AND F. E. CLEMENTS. 1939—Plant Ecology. New York.

DEPARTMENT OF BOTANY,
OREGON STATE COLLEGE,
CORVALLIS, OREGON.

A Brief Biographical Note on Edward Wilkinson

Hobart M. Smith and M. B. Mittleman

Chief among the collectors who have secured reptiles and amphibians in the state of Chihuahua, Mexico, is Edward Wilkinson. His collections were sent for study to E. D. Cope, who reported on them in two papers (1879:261-263; 1885:282-287) which included, among other novelties, the description of a very well defined species named for its collector (*Trimorphodon vilkinsonii*).

Although Wilkinson has contributed more to our knowledge of the herpetofauna of southern Chihuahua than any other collector, only little has been known of him. Through our interest in his collections from Mexico, particularly incited by the discovery among them of a lizard belonging to a remarkable species (*Urosaurus unicus*) otherwise unknown, we have made an attempt to learn something of his life, and more concerning his journeys in Chihuahua. Through the courtesy of Drs. Leonhard Stejneger, Alexander Wetmore, and Doris Cochran, we have been able to examine the records of the Smithsonian Institution for information concerning Wilkinson. From these we learned of his association in the later years of his life with a museum in Mansfield, Ohio, where we later pursued this investigation.

A considerable collection of historical relics and natural history specimens, largely amassed by Wilkinson, is on deposit on the top floor of the three-storied Soldiers and Sailors Memorial Building of Mansfield, Ohio. Through the kindness of Mr. F. Thane Shaw, custodian of the building, we were permitted to make two visits to the museum during closed hours; one of only a few hours' duration, the other of a full day. Mr. Fred E. Elder, in direct charge of the collection, courteously allowed us to examine specimens, furnished us with the photograph of Wilkinson here reproduced, and was of great aid in bringing to light certain information concerning Wilkinson's life. To these men we are greatly indebted for making our visits pleasant and profitable.

The notes taken by us on the small Chihuahua collection at Mansfield may be presented elsewhere; here we are concerned chiefly with a few facts concerning Wilkinson's life. Most of these have been gleaned from a Federal Writer's Project of recent date, to which Mr. Elder very kindly gave us access. Certain other facts concerning the Wilkinson collections which are not of interest here, have already been published by one of us (Mittleman, 1942:171-173).

Edward Wilkinson was a native of Mansfield, born in 1846 to the Rev. James and Jane Wilkinson. He was trained as a sheetmetal worker, at which trade he became expert. That he became a competent amateur naturalist in spite of the lack of tutelage is a tribute to his enthusiasm and aptitude for

Fig. 1. Edward Wilkinson, *circa* 1880.

natural history. His interest in that subject became apparent when he was quite young, and, so far as our records show, grew without benefit of that stimulus of association with trained naturalists that has figured so prominently in the direction and early development of so many of the more famous men in this field. What would have been the result had such a stimulus been present during Wilkinson's earlier life, one can only guess.

His career was interrupted by the Civil War, through which he served. Some time after the war was over, in 1873, his first opportunity to visit Mexico arose through an invitation from his brother, who was employed in certain mining operations in Batopilas, Chihuahua. Edward spent two years there, working with his brother and collecting specimens of many different groups of animals. His return to Mansfield was occasioned by the ill health of his mother, in 1875. Ten years later, in 1885, he returned to Chihuahua, prepared to do more extensive collecting than on the previous occasion. This second journey was spent largely in the vicinity of the City of Chihuahua. He returned to Mansfield after a short stay in Mexico.

Having devoted most of his spare time to the collection of relics of prehistoric ages and early settlements of Ohio, and of oddities of literary, historical, military and scientific character, as well as of diverse forms of animal life, he amassed such a quantity of material that he combined his various collections with those of Dr. J. R. Craig and others and organized the Mansfield Memorial Museum, on October 12, 1891. Wilkinson was appointed curator at that time, and retained the position until July 18, 1905. During this period he worked solely in the Museum, identifying collections, arranging new acquisi-

tions, and attending to the multitudinous other duties that confront the museum curator — and especially one in charge of such a varied collection. His care and the tremendous amount of personal labor invested in the Museum is clearly evident today, in the neatly labelled entomological collections, the sealed jars of specimens of numerous other groups of invertebrates, the elaborate collections of Indian relics, and not least, the cabinets themselves. Wilkinson's duties as curator involved not only the usual ones of cataloguing and arranging, but also those of carpenter; he constructed all the cases, cabinets and display racks in which the specimens are housed.

What Wilkinson's connection with the Museum may have been after his resignation on July 18, 1905, is not apparent. However, on August 19, 1908, he presented his entire personal collection to the G. A. R. McLaughlin Post No. 131, of which he was a member. The Museum has subsequently been cared for by the G. A. R. veterans. Ten years later, in 1918, Wilkinson died.

The Museum has not greatly changed since Wilkinson's death. It is given sympathetic care, but it is not notably added to or revised, as time passes. It was damaged somewhat in 1928 when an adjoining theatre burned. A redecoration removed all evidence of the fire, but the floor space was lessened in the process and the specimens were shuffled about considerably. Some of the labels were switched and some material lost or completely destroyed. The Museum was reopened on January 1, 1933.

REFERENCES

COPE, E. D. 1879—Eleventh contribution to the herpetology of tropical America. Proc. Amer. Phil. Soc. **18**:261-277.

———1885—Thirteenth contribution to the herpetology of tropical America. Proc. Amer. Phil. Soc. **22**:271-287.

MITTLEMAN, M. B. 1942—A summary of the iguanid genus *Urosaurus*. Bull. Mus. Comp. Zool. **91**(2):106-181, figs. 1-11, pls. 1-16.

UNIVERSITY OF ROCHESTER,
ROCHESTER, N. Y.

AND

NEW YORK, N. Y.

Notes and Discussion

The Yield of Certain Oyster Lands in South Carolina

G. Robert Lunz, Jr.

The tidal region of South Carolina from Charleston northeastward to the South Santee River is mainly low marsh land drained by numerous small intercommunicating creeks. These finally make their way to the sea through one of the several inlets opening to the ocean between the low sandy barrier islands which form the sea-face of the area. Scattered throughout the marsh land are a number of small creeks, sounds, and tidal flats. Three small rivers are included in this maze of waterways but they extend inland for only short distances. The Intracoastal Waterway, constructed by the Corps of Engineers of the War Department, cuts through this area and runs almost in a straight line from northeast to the southwest. There are 71,831 acres of marsh land in the region.

A large part of the region is productive of oysters and practically every creek bank is lined with oyster beds, most of which lie between high and low water marks. Twice daily these oysters are covered with water by tidal action. The range of tide in the region is from 5.2 feet (mean) to 6.1 feet (spring) at Charleston, S. C. The current velocity is roughly estimated to be from 2 to 3 miles an hour.

The salinity of the water in this coastal region of South Carolina is influenced by: (1) general meterological conditions; (2) the enormous volume of fresh water brought down by the Santee River (drainage area of 15,700 square miles), some of which is now diverted, via the Cooper River, through Charleston Harbor by the construction of the Santee-Cooper Power Dam; (3) general land seepage; (4) evaporation in the sounds and tidal flats; (5) land drainage into the three small rivers which extend inland; and (6) tidal action. These factors cause a seasonal, daily, and hourly fluctuation in salinity of the water. A series of 256 water samples taken over a period of years and covering all seasons of the year shows that the average salinity is 26.13 parts per thousand. The maximum salinity recorded was 34.51 parts per thousand; the minimum was 6.56. A series of nine 12-hour samples (that is, one sample taken each hour over a twelve hour period) shows that in most places the salinity is definitely correlated with the stage of the tide. In a few places (near the mouth of the Santee River) salinity is inversely proportionate to the height of the tide. The average fluctuation in these nine samples was 13.56 parts per thousand from the highest to the lowest salinity reading during a tidal cycle. The maximum fluctuation was 24.30 parts per thousand and the minimum was 0.80 parts per thousand.

An examination of any of the oyster beds in the area between Charleston and the South Santee River indicates that the percentage of dead oysters is not abnormally large. One hundred and ten samples (standard one square yard samples) taken throughout the region in 1936 showed that 10.87 percent of the oysters were dead (a dead oyster in these samples was defined as one being still joined at the hinge but without the living meat of the organism within the valves). Another group of 117 samples taken in 1942 and 1943 showed that 9.11 percent of the oysters were dead. It is believed that these oysters died a natural death or were killed by some pest or disease. The common oyster pests in South Carolina are: the boring sponge, *Clione celata* and *C. vastifica;* the oyster drills, *Urosalpinx cinereus* and *Eupleura caudata;* the conch, *Busycon carica;* the annelid worm, *Polydora ciliata;* and occasionally, the common starfish *Asterias forbesii.* Of these the boring sponge is the most serious because damage from the sponge is so great that it prevents the cultivation of oysters below low water mark except in a few limited places.

Within the area discussed in this paper the cultivation of oysters for canning is extensive. Each year some 250,000 bushels of shells are scattered between high and low water marks as cultch. The shells are usually "planted" in May and June and a

host of small oyster spat attach almost immediately. Studies made in 1936 show that from July 1 to 13, according to a count of 80 samples, 1.48 spat set per square inch of clean shell. From June 24 to July 14 (20 days) 140 samples showed that 1.44 spat set per square inch of clean shell. In 47 days from May 28 through July 14 a count of 80 samples showed that 4.50 spat set per square inch. From May 11 to July 10 (60 days) an examination of 80 samples showed a set of 7.10 spat per square inch. For a period of 87 days from May 28 to August 24, according to 70 samples, the set of spat was 2.73 per square inch. Later in the year after the spawning and setting season was virtually over a count of 170 samples showed that from September 12 to October 7 only 0.76 spat set per square inch of clean shell surface. From these and subsequent observations in this region of South Carolina the number of young oysters which attach to fairly clean shell seems almost to be limited only by the area of the shell. These young oysters grow rapidly until over crowding and a lack of food kill off some, but within two years they are usually ready for the market. The over crowding of the young oysters on the cultch allows them to develop but poorly and then only into misshapen "coon" oysters. However unattractive these oysters may be for the high class half-shell trade, they are commercially very valuable for canning purposes and this 47 mile strip of Carolina Coastline produces something over two million ounces of canned oyster meats each season.

During 1942 and 1943, the majority of the creeks and rivers within a half mile on either side of the Intracoastal Waterway were intensely studied and actual measurements were made of the length and width of the oyster beds. Thus in addition to a general knowledge of the region, the extent of the oyster beds is fairly accurately known along a path about one mile wide running for over forty miles through this coastal region from Charleston to the South Santee River. Taking 18 locations at random from this mile wide measured strip, an estimate of the percentage of creek and river edges that are productive of oysters can be made. In these 18 samples a total of 535,158.2 square yards of creek edges were measured. Of this amount 179,769.2 square yards were found to be covered with oysters. Thus 33.59% of the various waterways which are theoretically capable of producing oysters actually do yield oysters. The most densely populated sample was 92.02% covered with oysters and the most sparsely populated area was only 9.55% covered with oysters. Naturally there are some creek edges not bearing any oysters but by taking a total of 18 samples of fairly large size throughout the area it is believed that these barren spots have been accounted for and the estimate is therefore reasonably accurate.

From 117 samples of one square yard each taken throughout the entire region, it was found that each yard averaged 135.9 oysters two inches long or better (measurement from hinge to bill). Of these 9.11% were dead when the sample was taken. These same samples showed that each yard of oyster bottom would yield 0.54 bushel of live oysters two inches or more in length.

The entire region from Charleston to the South Santee River is 71,831 acres. Of this, 11,696 acres do not produce oysters because of the low salinity of the water near the mouth of the Santee River. Thus 60,135 acres of marsh lands and creeks are in the oyster producing lands that are within the region, studies were made of 15 random square mile samples. Air compilation sheets on a scale of 1 to 10,000 were used. A square mile was laid off at random on these sheets and the proportion of creek edges to marsh land was calculated. For all rivers and creeks in these samples the length of the creek or river was multiplied by 15 feet (taken to be the average width of an oyster bed) to give the area in square feet theoretically capable of oyster production. The average of the twelve samples showed that 1.86% of the area was made up of creek shores. Based on these figures the entire region from Charleston to the South Santee River has 1,118.5 acres of bottom which in theory are capable of producing oysters.

From actual field measurements, mentioned previously, it was found that 33.59% of the waterways actually bore oysters. Thus it can be calculated that there are 375.7 acres of oyster producing lands within the region. On this basis of 0.54 bushel of live oysters to the square yard, the region between Charleston and the South Santee River should produce 981,929.5 bushels of oysters.

There are no available commercial fishery statistics for the production of oysters in this part of South Carolina. The statistics for Charleston County, of which this region is a part, and information supplied by the Shelmore Oyster Products Company which operates in the area, indicate that the yield of oysters as given in this paper is about twice that actually gathered yearly. In the estimated yield all oyster beds in the region are included but actually some of these beds are so inferior, the oysters are so small, and the beds are so inaccessible that the oysters which they produce are not harvested. Again, the yield is calculated in this paper on the basis of 0.54 bushel per square yard but the oysters measured are two inches or more in length. According to law, oystermen are prohibited from taking more than 10% of their oysters less than three inches in length. Although this size factor would appear to be the prime cause for a difference in figures, observations seem to indicate that the size factor is not as significant as it may appear. Finally, some of this difference is due to the fact that the region is not developed to its fullest commercial possibilities.

CHARLESTON MUSEUM,
CHARLESTON, S. C.

The Family Euphorbiaceae: When and by Whom Published

Leon Croizat

The pages of this periodical have recently carried (in op. cit. **30**:456-503. 1943) a painstaking work by Wheeler devoted to listing the genera of the living *Euphorbieae*. In this work, the *Euphorbiaceae* are referred to the authorship of Jaume-St.-Hilaire (Exp. Fam. Nat. Plts. **2**:276 Pl. 108. 1805).

The fundamental nature of Wheeler's contribution to the bibliography of the *Euphorbiaceae* renders it very probable, that authors interested in this Family will turn to the pages of this periodical for additional corrections or data. In this anticipation, it seems necessary to call attention upon a reference which, overlooked by Wheeler, is bound to prove most troublesome to any botanist who happens to find it. The value of this reference, as it will readily be seen, greatly exceeds that of a bibliographical amenity.

In 1805 ("An XIII" of the French Revolutionary Era, in part) the *Euphorbiaceae* were independently published by two authors, as follows: (1) Jaume-St.-Hilaire, as cited above; (2) Lamarck & De Candolle, Fl. Franç., 2nd ed., **3**:327.

Internal evidence to settle the priority of these publications is unsatisfactory or lacking. The first volume of Jaume-St.-Hilaire's bears in the Preface (p. 7), the date "9 Ventose An XIII," which very nearly corresponds to March 1st, 1805. Lamarck & De Candolle's "Flore Française" is undated in the introductory matter, and Williams contributes little light (in Jour. Bot. **34**:431. 1896) as to the actual publication of all its volumes, but the last. Labillardière speaks of the "Flore Française" in a manner (in Ann. Mus. Hist. Nat. **6**:451. 1805 [XIII]) that may be construed to indicate that this "Flore" was out of press in June 1805. The issue of priority between the work of Jaume-St.-Hilaire and Lamarck & De Candolle, consequently, seems to involve less than two to three months.

Such facts as can be learned from other sources indicate that the matter is not quite as close as internal evidence suggests. Jaume-St.-Hilaire's work was actually published in *March 1805* (see: Intelligenzbl. Allg. Lit.-Zeit. **1805**:427. 1805, offering the "Exposition des Familles Naturelles" for sale before April 3rd; Jour. Gén. Litt. France **1805**:36. 1805); Lamarck & De Candolle's "Flore" was only out *in September 1805* (see: Jour. Gén. Litt. France **1805**:260. 1805). The publication was intended for the beginning of 1805 (op. cit. 261), but was delayed by corrections, which may account for Labillardière's statements.

It is fortunate that the reference to Jaume-St.-Hilaire's publication proves to be the earlier, for the reference to Lamarck & De Candolle's is almost entirely overlooked. Even Duby, in the "Botanicon Gallicum," which is based on the data and the material

of De Candolle, fails (op. cit. 411. 1828) to refer to the "Flore Française," giving an erroneous reference to "Euphorbiaceae Juss. gen. 384."

A peculiar attempt at *natural* classification, entirely overlooked so far, was made by Amos Eaton, who is generally believed to have been an uncompromising supporter of the Linnean artificial system. Being out of sympathy with the work of A. P. De Candolle and other systematists who, in his opinion, had treated A. L. de Jussieu with scant regard, Eaton decided to reintroduce the Jussieuan names for groups called Orders, but of variable taxonomic scope. In furtherance of this purpose, Eaton (Man. Bot. North Am., ed. 6, Part Second, 111, 1833) has "Order XCVI. Euphorbeae," this being an incorrect rendering of Jussieu's *Euphorbiae*, with two subdivisions of unspecified rank, "A. *Euphorbiaceae*," "B. *Empetreae*." Eaton's classification is mere bibliographical curiosity insofar as the *Euphorbiaceae* are concerned, but is well worth knowing to students of other Families, and of botanical history in general. Eaton's classification, as a matter of fact, would seem to be the earliest All-American product of natural systematic thought.

ARNOLD ARBORETUM,
HARVARD UNIVERSITY,
JAMAICA PLAIN, MASS.

Walker Prizes in Natural History, 1944, For Essays on Reptiles

Two prizes, founded by the late Dr. William Johnson Walker, are offered annually by the BOSTON SOCIETY OF NATURAL HISTORY for the two most acceptable papers written in the English language, on a subject chosen by the Board of Trustees of the Society.

PRIZES: A prize of sixty dollars may be awarded to the author of the best essay. This award may be increased to one hundred dollars, at the discretion of the judges of the contest, in the case of a paper of exceptional merit. A second prize of fifty dollars will be given only if the next best paper seems worthy of the distinction. No prize will be awarded unless the papers submitted are deemed worthy by the judges.

ELIGIBILITY: The competition for these prizes is not in any way restricted.

SUBJECT MATTER: Each paper must be the result of original and unpublished research personally conducted by the author and accompanied by an accurate bibliography and a review of general literature on the subject. All papers must be typewritten and in complete form for publication. Other things being equal, preference may be given papers showing evidence of preparation especially for this competition.

AUTHORSHIP: Each paper must be anonymous. It must bear a pseudonym placed in a conspicuous place on the first page. A sealed envelope, also inscribed with this pseudonym, must accompany the manuscript. The contents of this envelope will divulge the identity and address of the author. Anything in the essay which shall furnish proof of the identity of the author shall be considered as debarring the paper from competition.

CLOSING DATE: All competitors must submit their work to the Secretary, Boston Society of Natural History, 234 Berkeley Street, Boston, Massachusetts, before May 1, 1944.

The Society and the judges assume no responsibility for publication of the winning papers. However, it is understood that authors should not publish their papers until after the announcement of the prize awards at the Annual Meeting of the Society in October, 1944.

—Charles H. Blake, *Secretary*

BOSTON SOCIETY OF NATURAL HISTORY,
234 Berkeley Street, Boston, Massachusetts,
October, 1943.

Subject for 1945: *Any subject in the field of mammals—*

Book Reviews

A Short History of the Plant Sciences. By Howard S. Reed. A New Series of Plant Science Books edited by Frans Verdoorn, Volume VII. Chronica Botanica Co., Waltham, Mass. 1942. x + 323 pp., 37 figs. Buckram, $5.00.

In the opening paragraph of the Introduction the author conveniently absolves himself of dealing in this book with certain plant sciences and various aspects of others, either because they are supposed to have been treated adequately in other books or simply because they did not arouse sufficient interest in the writer. Apart from the fact that such reasons are both incorrect and misleading, this easy solution defeats at once the real aim of the author, stated in the second paragraph of the Introduction, namely to provide "for the average graduate student in our universities" a guide "to a better understanding of past and present trends" (p. 6). With such important sciences as systematic botany, phylogeny, genetics and others completely omitted or treated only in a cursory manner, graduate students are bound to get a wrong perspective and spotty knowledge.

The illustrious name of Johann Gregor Mendel, for instance, appears once on the last page (p. 309) in Chapter xx (one page long) in very small type together with other names in a list of 50 (?) distinguished botanists but is absent in the text as well as in the index. If Mendel's name can be sacrificed in favor of those of many lesser lights, why would it not be equally logical to exclude that of Linnaeus too? After all, general botany textbooks sketch the accomplishments of Linnaeus and Mendel even for the beginning student. But why should so many important historical details be eliminated by such disproportionate treatment and subjective evaluation of the past and present trends? Despite the over-emphasis on physiology (chapters 12-17 inclusive), many significant developments are omitted, e.g., plant tissue culture, pigmentation in algae and others. Some sciences seemingly stopped their development with the turn of this century, plant geography for example, presumably because the author was unwilling to familiarize himself with these fields to the extent that he could prepare a satisfactory outline of present trends. Although such chapters or parts may be difficult to write, they would be of inestimable value to graduate students and botanists in general.

The algae are ignored with the exception of casual references to syngamy in some forms or to the structure of the cell wall in *Valonia*. The newer knowledge of alternation of generations in algae is disposed of as too confused in a short paragraph (p. 140) in the chapter on Morphology. Why is not the same line of reasoning applied to certain physiological problems, the discussion of which requires page after page but leaves the reader with no better results? Plant classification culminates with de Jussieu's system (p. 102) and the student is once more left to his own ingenuity. For, if the histories of the plant sciences omitted from this book have been presented elsewhere, the student will still be at a loss to find them, since no references are provided for this purpose. The reader will also look in vain for information on the earliest herbaria, scientific botanical journals, reference works like the Kew Index, research institutes, botanical societies, etc.

A comparison with its counterpart suggests itself. Möbius' *Geschichte der Botanik* (Jena, 1937) was written from the same point of view, i.e., to provide a history of botany by subjects and plant sciences with limited biographical details of botanists. Of the two books, Möbius' history, despite some minor shortcomings, gives the student a much better appreciation of all plant sciences and their respective developments. Characteristically Reed does not cite Möbius' history, though he seems to be familiar with his work on plant pigments.

An amusing misprint appears an page 314, where Schleiden's famous textbook is given a new title.

If the reader appreciates that fact that this is at best "A Short History of *Some* Plant Sciences," the book can be read with interest and some degree of benefit. "A Short History of *the* Plant Sciences," however, is not yet available.—Theo. Just.

THE CYTOPLASM OF THE PLANT CELL. By Alexandre Guilliermond. Authorized Translation from the Unpublished French Manuscript by Lenette Rogers Atkinson. Foreword by William Seifriz. A New Series of Plant Science Books edited by Frans Verdoorn, Volume VI. Chronica Botanica Co., Waltham, Mass. 1941. x + 247 pp., 152 figs. Buckram, $4.75.

As a rule, textbooks of cytology are predominantly concerned with nuclear phenomena and to a much lesser extent with the cytoplasm and its constituents. The publication of Professor Guilliermond's monograph on *The Cytoplasm of the Plant Cell* is, therefore, a significant event. First of all, this book can readily be regarded as a critical and inclusive presentation of the many scattered and frequently contradictory details and views making up our present knowledge of the cytoplasm of the plant cell. In addition, this monograph is probably the last major botanical contribution to come from France for the time being and is in keeping with her great tradition in botany.

The notable researches of Professor Guilliermond and his students are conspicuously represented but without detracting in any way from the recognition and evaluation of the contributions made by others. Such unbiased treatment on part of the author is particularly praiseworthy in view of the many highly controversial subjects and structures discussed by him, such as mitochondria, Golgi apparatus, etc.

Cytologists accustomed to looking at expensive plates will be somewhat surprised to see the rather inexpensive illustrations. Few of these, however, will be found inadequate.

As a whole, the translation is very satisfactory. An occasional long sentence could have been handled differently, as for instance the first paragraph of Chapter X. For the sake of clarity, French and/or German terms are often retained in the text. It is regrettable that no subject index was prepared to accompany the others of author, plant and animal names.

Geneticists would probably enjoy reading an equally critical chapter on cytoplasmic inheritance and the genetical importance of the plastids. Otherwise the book can be used by botanists and zoologists alike, all of whom are greatly indebted to the author for this excellent monograph.—THEO. JUST.

ORGANISERS AND GENES. By C. H. Waddington. Cambridge Biological Studies. Cambridge University Press; Macmillan, N. Y. 1940. xi + 160 pp. 15 figs. $3.00.

Although there may be a few who still regard themselves embryologists, or geneticists, or taxonomists, or physiologists, etc., it is rapidly becoming plain to most that there are fundamentally no sharply delimited fields of study as embryology, or genetics, or taxonomy, or physiology, etc.—there is only Biology. The older notion of segregation of Biology into subsciences and of each man's sticking to his last undoubtedly was the effect of the study of end-products; and equally undoubtedly have the investigators in these useful and convenient subdivisions contributed magnificently. When one turns his attention, however, to the steps preceding the end-product, the lines of demarcation between the different arenas are seen for what they really are—arbitrary boundaries which fade and lose their significance upon close examination. Certainly two of the most closely related topics are genetics and embryology; and even if it had no other merit, Waddington's book is important because it demonstrates clearly the interdependence of the results of the studies in these two fields.

The small volume, however, stands for more than that. It is admittedly circumscribed and limited in scope ("it is an account of the lines of thought suggested by a single set of phenomena, those of embryonic induction"), but the author develops well his thoughts based on nicely chosen evidence drawn mostly from the literature in experimental embryology from 1930-39. Short summaries are given of: organisers in various vertebrates; evocation and individuation; competence; morphogenetic movements; organisers and growth; developmental patterns; and organization as such. In these embryological discussions the effects of genic actions are noted where possible and pertinent. Two chapters, "Genic Action" and "The Temporal Course of Gene Reactions," are mostly

genetic in nature. The latter chapter is especially important because in it is seen the most complete fusion of "Genetics" and "Embryology."

This compact book on early development and the significance of genetic factors operating during this period is recommended to biologists, even to those not actively engaged in embryology and genetics.—E. LAWRENCE POWERS, JR.

SCIENCE IN PROGRESS. Third series edited by George A. Baitsell. Yale University Press, New Haven, Conn. 1942. xiv + 322 pp., 112 figs. $3.00.

Based on the National Lectureships of 1941 and 1942 of the Society of the Sigma Xi, the third series of "Science in Progress" is a fitting companion volume to its forerunners. Unlike many other publications devoted to the general purpose of scientific synthesis, this series has never been confined to a special field, however delimited, but has always been representative of many sciences. Of the ten contributions included in the present volume three are of immediate interest to biologists. V. K. Zworykin discusses "Image Formation by Electrons" and illustrates effectively what new knowledge can be expected through the use of the electron microscope in biology and other fields. "Some Fundamental Aspects of Photosynthesis" are reviewed by James Franck, who shows that photosynthesis as now understood must have had a predecessor which operated without the aid of a pigment. In addition, he proposes a series of photochemical and catalytic reactions, nine in all, which admittedly suggest the sequence of events rather than the final story. In "Mode of Action of Sulfanilamide" Perrin H. Long summarizes ably the present status of knowledge regarding this and related drugs.

As continuance of this valuable series seems assured, it is safe to look forward to contributions in sciences such as embryology, entomology, paleontology and others so far not represented despite their great importance and advances.—THEO. JUST.

ERD- UND LEBENSGESCHICHTE, EINE EINFÜHRUNG IN DIE HISTORISCHE GEOLOGIE. By Karl Beurlen. Quelle und Meyer, Leipzig. 1939. viii + 462 pp., 227 figs., 29 tables. RM 15.00.

This book is meant to be an introduction to the field of historical geology and for this reason the subject indicated in the first part of its title occupies most of its pages. The stratigraphical part of the book is well written, interesting and stimulating. Most of the descriptions are based on central European conditions and in describing them the author purposely neglected details which might confuse the reader, sometimes to the extent of presenting a rather complex condition in almost ideally simple terms.

The sketch of the history of life is by far not as enjoyable as that of the earth. To a geologist the understanding of the historic development of organisms is no aim in itself. It is only of interest in so far as it might assist, as a *tertium comparationis*, in the solution of stratigraphical problems. In the light of this fact the obvious inequality in the treatment of the topics—the history of the earth and that of life—might appear pardonable.

It is rather easy to criticize a book of this sort, since there is hardly a man who can master both fields, geology and biology, with equal thoroughness. This being the case, however, one might expect the author to ask a colleague in the other field to read over the manuscript in order to eliminate errors for which there is hardly any excuse. Particularly strange in this connection is the author's account of the formation of the lungs in the early tetrapods (p. 210): "Of the original gill pouches formed by the pharynx only the last pair remains. This does not break through to the outside but becomes elongated backwards into the thorax. Thus a new respiratory organ originates, . . . i.e., a lung."

For the beginning student, primarily interested in geology, the book draws a vivid picture of the lithogenetic and diagenetic processes and of the historical development of the multitude of surface phenomena of the earth's crust.—RAINER ZANGERL.

JOSEPH GRINNELL'S PHILOSOPHY OF NATURE. Selected Writings of a Western Naturalist. Preface by Alden H. Miller. University of California Press, Berkeley and Los Angeles. 1943. xv + 237 pp., frontispiece, 10 figs., two colored plates. $2.00.

It is an irretrievable loss to biologists that death prevented Joseph Grinnell from carrying out his promise to write a general book on geography and evolution. Written by the leading American naturalist of his time, this book would not only have been his scientific legacy but a milestone of biological thought, methodology, and guide for future work. In its place his associates published the present volume of selected writings in tribute to their distinguished master and in commemoration of the Seventy-Fifth Anniversary of the Founding of the University of California.

These selected writings are fortunately and reverently reproduced in Grinnell's original version and reflect admirably the wide interests, observations, thoughts, and activities of their author. They also bear out that keen powers of observation trained on wild life in nature can yield profoundly significant results which need not clash with those obtained by more fashionable experimentation. Sovereign knowledge and wisdom were the outgrowths of these continued observations on vertebrate life in the diversified environments of California and neighboring states. Although his attainments are numerous, notable, and exemplary, "Philosophy of Nature" portrays the man Grinnell and discloses his principal thoughts for the lasting benefit of his many students and all those who still have faith in the real "naturalist."—THEO. JUST.

INTRODUCTION TO PARASITOLOGY. By A. S. Pearse. Charles C. Thomas, Springfield, Ill. 1942. ix + 357 pages, 448 figures. $3.75.

This volume could well have been entitled "Consortism" or perhaps "Parasitism, Symbiosis, and Commensalism." The presentation of the subject is extremely general and often excludes very fundamental information which better students profoundly appreciate. A general discussion of theories in regard to the origin of parasitism, more complete information on distribution, charts or tables summarizing heterogeneous information, more detail in regard to symptomology and therapy, together with clear-cut generic distinctions between different parasites (e.g. Protozoa) would constitute valuable additions.

In a list of "Groups of Animals in which Parasites Occur" sixteen groups are included in which "no parasites occur" and which could advantageously have been deleted for more valuable information. The author conveys the opinion that trypanosomes live only in the blood when in vertebrate hosts. This is not the case with *Trypanosoma cruzi* which becomes an intracellular parasite of various tissues. The well-recognized haemosporidian *Plasmodium ovale* is omitted as is *Uncinaria stenocephala* with reference to creeping eruption. The Law of Priority which states that "the earliest name given to a genus or species is the only valid one" requires, among other things, that the name be published and accompanied by a description, indication, or definition, and the use of the rules of binomial nomenclature in the formulation of the name.

Although the book contains much valuable information and is excellently illustrated, it seems that an ill-fated attempt was made to include too much in such a short treatise. It is unfortunate that the very brevity of the volume prevents inclusion of the wealth of information which is at the author's command.—JOHN D. MIZELLE.

WILD VIOLETS OF NORTH AMERICA. By Viola Brainerd Baird. With Color Illustrations by F. Schuyler Mathews. Introduction by Herbert L. Mason. University of California Press, Berkeley and Los Angeles. 1942. xv + 225 pp., 80 color illustrations, 19 figs. $10.00.

The publication in 1942 of this beautiful book should gladden the hearts of all botanists and plant lovers. First, it is still possible to have colored illustrations of plants made by a botanical artist and published without loss of detail or discoloration. Secondly,

the book is scientifically sound, being the product not only of the author's labor of love but also of her serious scientific work. Using her father's material, she completed his life's work with reverence, ingenuity, persistence and competence. This strong personal note is expressed also in the fact that the whole edition of 1,000 copies was autographed by the author.

The treatment strikes a happy medium between the best type of popular presentation and scientific accuracy. The bibliography, for instance, contains for each species all scientifically important data such as the reference to the original description, synonyms, the type collection and locality. By comparison the descriptions are simple and as non-technical as possible, though always accurate. The colors are often specified in Ridgeway's terms (in parentheses). Suitable keys are included as are a key to colors and some distributional maps. The price is certainly low in view of the great cost of production and excellent workmanship of the University of California Press.

One statement in the Preface (p. ix) must be amended. Major John Eatton LeConte's set of colored illustrations of eastern violets and certain other plants, rescued from oblivion by Edward Lee Greene and deposited at the University of Notre Dame, *was made available* for general use by the Rev. J. A. Nieuwland, C.S.C. The latter edited LeConte's monographs and published them in 1917 as Reprint 5 of the *American Midland Naturalist* together with 42 photographic copies of unpublished plates (and two extra plates made from originals in the New York Botanical Garden). If desired, these sets were furnished with hand-colored photographic copies.—THEO. JUST.

A HANDBOOK OF PLANT TISSUE CULTURE. By Philip R. White. The Jaques Cattell Press, Lancaster, Pa. 1943. xiv + 277 pp., 71 figs., three tables. $3.75.

Compared with the rather spectacular development and successes of animal tissue culture in recent years, plant tissue culture has matured rather slowly and quietly. The publication of the present handbook, written by one of the foremost investigators in this field, marks a turning point in the progress of plant tissue culture.

The book begins with a discussion of morphogenesis, the study of which led to the development of tissue culture techniques. A historical review of plant tissue culture, interestingly illustrated with portraits of most of the men who have made notable contributions to this field, follows. Other subjects treated are: living materials suitable for the preparation of tissue cultures, the laboratory and its equipment, standard procedures for the preparation of nutrients, procedures for obtaining aseptic tissues (seeds adventitious roots, cambium, and others), culture techniques, and growth measurements and their interpretation. Two chapters concerning the application of tissue culture to the study of pathological, physiological, and morphogenic problems conclude this excellent handbook. A bibliography of 457 references and an adequate index are appended.

Since the material is well organized and the subject matter is presented with clarity and conciseness, this authoritative handbook is not only a highly reliable but also a practical guide for the research worker and is likely to be of special service to all those not actively engaged in tissue culture.—N. L. NOECKER.

GEOGRAPHICAL GUIDE TO FLORAS OF THE WORLD. An Annotated List with special reference to useful plants and common plant names. Part I. Africa, Australia, North America, South America, and Islands of the Atlantic, Pacific, and Indian Oceans. By S. F. Blake and Alice C. Atwood, U. S. Department of Agriculture, Miscellaneous Publication No. 401, Washington, D. C. 1942. 336 pp., cloth bound. $0.75.

Bibliographies are often more badly needed than available. This *Guide* is a good example, as is evident from the authors' own statement: "No list of the scope of this one has ever been published." If Part II should follow soon, botanists and others needing information about the plants of any region will be permanently indebted to the authors for their eminently useful and timely *Guide*.

Admittedly selective, this bibliography does contain all important references, which are grouped by countries or areas either as general or local. The list also reveals clearly the great gaps in our knowledge of the plant life of many countries, including several states of the Union, as well as the unequal character of the available publications. A master list of the most useful 100 floras and floristic works is presented in the Introduction. The abbreviations of the periodicals cited are found at the end of the book together with author and geographical indices.

Though the manuscript was completed through 1939, certain significant works published later are listed in footnotes. Others, it is hoped, will be included in Part 2 or in a supplement. The list is confined to works dealing with vascular plants in general but contains many valuable references to useful plants and vernacular names. In as much as the authors examined all of these publications, they were able to annotate the list and point out many "common faults and omissions in the preparation of floristic papers." Botanists will do well to observe these suggestions as well as to visit the many botanically unknown or incompletely known countries in a concerted effort to conclude the age of botanical exploration.—THEO. JUST.

A HANDBOOK OF MEDICAL LIBRARY PRACTICE, Including Annotated Bibliographical Guides to the Literature and History of the Medical and Allied Sciences. Compiled by a Committee of the Medical Library Association, Janet Doe, Editor. American Library Association, Chicago, Ill. 1943. x + 609 pp., illus. $5.00.

Obviously intended for the use and benefit of medical librarians, students and investigators using medical libraries, the eight contributions included in this handbook cover all important aspects of organization, management, equipment and reference work. Prepared by a Committee under the able editorship of Janet Doe, these contributions disclose the special problems encountered in the operation of medical libraries and reflect the great experience in dealing with them acquired by the authors.

It is very difficult to single out chapters, which might be more useful than others. Certainly the reader will benefit most from Chapters VII and VIII with their carefully classified lists of historically important works and reference books from the wide range of subjects included in the scope of large medical libraries. Zoological literature is well represented, whereas certain botanical aids are missing. The most valuable of these would be the *Botanical Review*, *Fortschritte der Botanik*, and *Bibliography of Agriculture* (published by the Library of the U. S. Dept. of Agriculture). Surprising also is the omission of the very pertinent writings of the late Professor Raymond Pearl and of C. W. Dodge's *Medical Mycology*. An extensive Index concludes this very serviceable and informative volume.—THEO. JUST.

DUNE BOY, THE EARLY YEARS OF A NATURALIST. By Edwin Way Teale. Dodd, Mead and Co., New York. 1943. viii + 255 pp., woodcut illus. $3.00.

The area most distinguished for physiographic, botanical, and faunistic interest in the immediate vicinity of Chicago is the dune region at the southern end of Lake Michigan. That this is the scene of the childhood experiences of an American naturalist of distinction provides a combination of interests in Mr. Teale's book for mid-western naturalists. It is a book that I find singularly appealing in this local interest, as well as in the broader aspect of the perennial story of a boy's relations with his environment.

Those of us who have the good fortune to have as our childhood background the mid-western farm at the turn of the nineteenth century (whether the year round or as a summer refuge with our grandparents) will feel an immediate bond with Mr. Teale, and with his farm grandparents who are so sympathetically described in this nostalgic book.

The Middle West, from Michigan and Ohio to Kansas and Nebraska, has traditions of food and cookery that form one of its shadowy distinctions as a province of the United States. Perhaps our mixture of races and of emigrants from the other American

provinces has contributed the variety of our food habits that gives us such gastronomic preeminence (Chapter XIII, Dinner Bells, and refer also to Della Lutes).

The more important aspect of Mr. Teale's reminiscences of a boyhood in the Indiana Dune country near Michigan City to the Midland Naturalist lies in the fact that he has made himself a naturalist, and that the origin and development of naturalists is one of our primary interests. With the freedom of the farm, with grandparents whose wealth of farm-lore was a distinctive kind of education, with the near-by wilderness of the Dunes, B.G.,* with an attic full of Youths Companions and other old magazines, what more could be asked for a budding naturalist? There *was* something missing. A little more intelligent direction of the boy's native interests, and of his collecting and museum building instincts, would have greatly furthered his development; it is the function of museums and of schools and colleges to discover and to foster such instincts; and the measure of the success of our several institutions may well be our success in finding and aiding those who are to be our successors.—KARL P. SCHMIDT, Chicago Natural History Museum, Chicago, Ill.

* Need I explain, Before Gary?

DICTIONARY OF SCIENCE AND TECHNOLOGY IN ENGLISH-FRENCH-GERMAN-SPANISH. By Maxim Newmark. Philosophical Library, New York. 1943. viii + 386 pp. $6.00.

"Containing 10,000 current terms in the English language most frequently used in the physical sciences and their applied fields, together with separate indices in French, German, and Spanish, conversion tables, and technical abbreviations," this multi-lingual dictionary is the direct outgrowth of the author's teaching experience in a polytechnical institution and of his desire to fill a conspicuous gap in available dictionaries. Particular emphasis is placed on terms used in such fields as aviation, radio, and television, most of which have been introduced quite recently and therefore can not be found in other dictionaries. No serious objection will be raised to such a noble and laborious enterprise. Actually, however, important metallurgical terms as well as many others are omitted and the various lists of abbreviations are incomplete. Perhaps the use of high school textbooks limited the basic scientific vocabulary despite the author's list of such valuable sources as special dictionaries, encyclopedias, and technical journals. Biologists will look in vain for simple terms such as bacteria, bone, flower, mammal, etc., although hemp, mahogany, walnut, yeast, etc. are included. In a new edition more biological terms, at least those in applied fields of biology such as bacteriology, forestry, etc. could be added with profit.

In view of the great service rendered by the author in compiling an up-to-date and useful dictionary in four languages, it is most regrettable that the book was printed on cheap stock, which compares very unfavorably with the type of paper used in standard dictionaries and which emphasizes unduly its relatively high cost.—THEO. JUST.

Science

A

Will

A S

Flor

New

Revi

Rece

Supp

Som

Age

Seas

Occu

Swin

A N

Post-

A Br

Note

Book

Science Library

JAN 7 1944

The

American Midland Naturalist

Devoted to Natural History, Primarily that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

Edited by Theodor Just

Contents

William Albert Setchell—Francis Drouet 529

A Study, Anatomical and Taxonomic, of the Genera of Rhododendroideae—Herbert F. Copeland 533

Flora of Jornada Experimental Range, New Mexico—Elbert L. Little, Jr., and Robert S. Campbell 626

New Species and Transfers in Myxophyceae—Francis Drouet 671

Revision of the Giant West Coast Land Slugs of the Genus Ariolimax Morch (Pulmonata: Arionidae)—Albert R. Mead 675

Records and Descriptions of North American Crane-Flies (Diptera) Part IV. Tipuloidea of the Yellowstone National Park—Charles P. Alexander 718

Supplementary Notes on Family Names in the Order Araneae—B. J. Kaston 765

Some Serranid Fishes of Texas, the Centropomidae, Moronidae and Epinephelidae—J. L. Baughman 769

Age Determination in Juvenal Bob-white Quail—George A. Petrides and Ralph B. Nestler 774

Seasonal Insect Food of the Western Chipping Sparrow—George F. Knowlton and Stephen L. Wood 783

Occurrence of Upper Canines in Mountain Sheep, Ovis canadensis—Seth B. Benson 786

Swimming, Feeding and Locomotion of a Captive Mole—Charles A. Reed and Thane Riney 790

A New Acanthodian Fish from the Upper Mississippian of Indiana—John W. Wells and Arthur H. Blickle 792

Post-Pleistocene Forest Succession in Northern Idaho—Henry P. Hansen 796

A Brief Biographical Note on Edward Wilkinson—Hobart M. Smith and M. B. Miittleman 803

Notes and Discussion

The Yield of Certain Oyster Lands in South Carolina—G. Robert Lunz, Jr. 806

The Family Euphorbiaceae: When and by Whom Published—Leon Croizat 808

Walker Prizes in Natural History, 1944, for Essays on Reptiles 809

Book Reviews 810

Vol. 30 NOVEMBER, 1943 No. 3

EDITORIAL STAFF

THEODOR JUST ..... *Botany*
Editor, University of Notre Dame

EDWARD A. CHAPIN ..... *Entomology*
U. S. National Museum, Washington, D. C.

CARROLL LANE FENTON ..... *Invertebrate Paleontology*
West Liberty, Iowa

JOHN HOBART HOSKINS ..... *Paleobotany*
University of Cincinnati, Cincinnati, Ohio

REMINGTON KELLOGG ..... *Mammalogy*
U. S. National Museum, Washington, D. C.

JEAN MYRON LINSDALE ..... *Ornithology*
Hastings Reservation, Monterey, California

GEORGE WILLARD MARTIN ..... *Mycology*
State University of Iowa, Iowa City, Iowa

KARL PATTERSON SCHMIDT ..... *Ichthyology and Herpetology*
Field Museum, Chicago, Illinois

HARLEY JONES VAN CLEAVE ..... *Invertebrate Zoology*
University of Illinois, Urbana, Illinois

NOTE: THE AMERICAN MIDLAND NATURALIST, published by the University of Notre Dame, is primarily, though not exclusively, devoted to the Natural History of the Middle West. A wide selection of papers on botany, paleontology and zoology is published in bi-monthly issues, three of which make up a volume.

Twenty-five reprints will be given free of charge provided, at least, an equal number is ordered. Authors are requested to submit carefully prepared manuscripts and to limit tables and illustrations as far as possible. Abstracts should accompany manuscripts.

The following numbers are out of print: vol. 1, (1, 5, 11, 12); vol. 2, (1-3, 8-10); vol. 3, (1-3, 5-12) index, title page; vol. 4, (1-7, 12) index, title page; vol. 5, (6-8); vol. 6, (5, 8, 9, 12) index, title page; vol. 7, (6); vol. 9, (9, 10); vol. 10, (11-12) index, title page; vol. 11, (1); vol. 12, (12); vol. 14, (1, 5). All others available, 30 cents per copy. Complete volumes: $3.00; volumes 7, 13, and 14, $1.50 each; vol. 15, $2.00, single issues, 35 cents; vol. 16, $3.00, single issues, 50 cents; vol. 17, $4.50, part 1, $2.00, nos. 2-6, 50 cents each; vol. 18, $3.00; single issues, 50 cents; vols. 19-29, $2.50 each; single issues, $1.00. Subscription price per year, $5.00.

Exchanges for journals, special volumes or duplicate books, and specimens should be arranged directly through the editorial office at the University of Notre Dame, where subscriptions also are received. Offers should accompany request for exchange.

For citation use this abbreviation: *Amer. Midl. Nat.*

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103, Act of October 3, 1917, authorized on July 3, 1918.

REPRINT-SERIES

(Reprints 1, 2, 3 were issued with volume 2, reprint 4 with volume 3 and reprint 5 with volume 5).

(1) RAFINESQUE, C. S.—Neogenyton. 1825 ..... $ .25

(2) ———The Natural Family of Carexides. 1840 ..... .50

(3) ———Scadiography of 100 Genera of Ombelliferous Plants, etc. 1840 ..... 1.50

(4) ———Monographie des Coquilles Bivalves et Fluviatiles de la Rivière Ohio. Remarques sur les Rapports Naturels des Genres Viscum, Samolus et Viburnum. A Bruxelles. 1820 ..... 1.50

(5) LECONTE, J. E.—Reprints of Monographs without plates 2.50

With 42 photographic copies of unpublished plates (7×8). ..... Prices on request

———Two extra plates reproduced from originals in New York Botanical Garden ..... Prices on request

PUBLICATIONS

AMMONS, NELLE.—A Manual of the Liverworts of West Virginia. 1940. Cloth ..... $ 1.75

BAILEY, V.—Cave Life of Kentucky. 1933 ..... 1.25

BARKLEY, FRED A.—Keys to the Phyla of Organisms Including Keys to the Orders of the Plant Kingdom. 44 pp., paper bound. Postpaid ..... .75

CONANT, R.—The Reptiles of Ohio. 1938. Cloth 2.00

GREENE, E. L.—Pittonia. A Series of Papers Relating to Botany and Botanists. 5 volumes. 1887-1905 ..... 14.00

———Manual of the Botany of the Region of San Francisco Bay. 1894. Bound cloth 2.00

Unbound 1.50

———Flora Franciscana. Part 2. 1895 ..... .75

———Plantae Bakerianae. 1-3. ..... 1.30

———Cybele Columbiana. A Series of Studies in Botany, chiefly North American. (All published). 1914 ..... .75

JUST, THEO. (Editor)—Plant and Animal Communities. 1939. Cloth 2.50

KISTLER, ELLEN D.—Bibliography of the Botanical Writings of Edward Lee Greene. 1936 ..... .25

SETTY, L. R. AND KENNETH W. COOPER—Studies in the Mecoptera. 1940 ..... 1.00

WEATHERWAX, J.—The Phylogeny of Zea Mays. 1935 ..... .50

THE UNIVERSITY OF NOTRE DAME

Notre Dame, Indiana, U. S. A.

The College of Arts and Letters

The College of Science	The College of Law
The College of Engineering	The Graduate School
The College of Commerce	The Summer Session

For a Bulletin or other information, address

THE REGISTRAR - - - - - Notre Dame, Indiana

PUBLICATIONS IN MEDIAEVAL STUDIES

VOLUME I—*The Works of Peter of Poitiers, Master in Theology and Chancellor of Paris* (1193 - 1205). By Philip S. Moore. 1936. Pp. ix-218. Cloth, $2.25; Paper, $1.75.

VOLUME II—*Commentarius Cantabrigiensis in epistolas Pauli e schola Petri Abaelardi: 1. In epistolam ad Romanos.* By Artur Landgraf. 1937. xlii-223. Cloth, $2.25; Paper, $1.75.

2. In epistolam ad Corinthios Iam et IIam, ad Galatas et ad Ephesios. By Artur Landgraf. 1939. Pp. i-221. Cloth, $2.25; Paper, $1.75.

VOLUME III—*Petri Pictaviensis allegoriae super tabernaculum Moysi.* By Philip S. Moore and James A. Corbett. 1938. Pp. xxiii-214. Cloth. $2.25. Paper, $1.75.

VOLUME IV—*Johannis Dominici Lucula Noctis.* By Edmund Hunt. 1940. xxxi-432. Cloth, $4.50. Paper, $4.00.

VOLUME V—*Sachsenspiegel and Bible.* By Prof. Guido Kisch. 1941. Pp. ix-198. Cloth, $4.00. Paper, $3.25.

VOLUME VI—*Saint Bernward of Hildesheim.* By Francis J. Tschan. 1942. Pp. vii-235. Cloth, $4.00. Paper, $3.25.

ADDRESS: Publications in Mediaeval Studies. The University of Notre Dame, Notre Dame, Indiana (U. S. A.)

The University Press, Notre Dame, Indiana